ABSTRACT

Title of Thesis: THE EFFECTS OF SUBMERGED AQUATIC VEGETATION AS HABITAT ON THE SURVIVORSHIP OF CLAMS: FIELD SURVEYS IN ST. MARY'S RIVER, MARYLAND AND LABORATORY PREDATION EXPERIMENTS

Carolyn Cristine Reid, Master of Science, 2003

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Submerged aquatic vegetation is a complex habitat that may strongly affect the survivorship of associated animal species. Location with reference to SAV and seasonal changes have been suggested as important factors influencing species' survivorship. A field study examining natural abundances during spring and summer was conducted to examine the SAV effect on clam survivorship in St. Mary's River, a Chesapeake Bay tributary. Data revealed that SAV biomass affected clam abundances in summer, but not spring. Crab pots caught significantly greater numbers of *Callinectes sapidus* (blue crab)

outside grass beds than inside SAV, contrary to published studies. Greater predation pressure on clams in lower SAV biomass may be causing differences in clam abundance. Experiments investigating *C. sapidus* predation on *Mya arenaria* (soft-shell clam) in different SAV densities indicated that SAV presence significantly reduced predation. Habitat studies tracking behavior revealed crabs spent more time in vegetation but consumed more clams outside SAV.

THE EFFECTS OF SUBMERGED AQUATIC VEGETATION AS HABITAT ON THE SURVIVORSHIP OF CLAMS: FIELD SURVEYS IN ST. MARY'S RIVER, MARYLAND AND LABORATORY PREDATION EXPERIMENTS

by

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Chapter 1. Introduction

Habitat complexity has been shown to significantly influence many ecological processes. Complex habitat has been associated with increased faunal abundance through many ecological processes including enhanced access to food (Peterson et al. 1984), reduced exposure to environmental stress (Kohn and Leviten 1976) and water currents (Irlandi and Peterson 1991), reduced predation risk (Orth *et al*. 1984, Wilson et al. 1987, Lubbers et al. 1990, Irlandi 1994), increased surface area in the benthos (Heck and Wetstone 1977), and decreased competition (Basquill and Grant 1998).

Submerged aquatic vegetation, or SAV, is a common habitat found in temperate shallow-water estuarine environments. This three-dimensional biotic environment provides surface area, cover, and structure for a number of animals. Research has documented increased animal abundance associated with SAV habitat (Heck and Thoman 1984, Peterson et al. 1984, Peterson 1986, Orth and van Montfrans 1987, Capehart and Hackney 1989, Rozas and Minello 1998, Scott-Denton 1999, Castellanos and Rozas 2001, Short et al. 2001). Protection from predators has been cited as one reason for increased faunal abundances within SAV habitat (Heck and Thoman 1982, Orth et al.

1984, Wilson et al. 1987, Lubbers et al. 1990, Wilson et al. 1990a, Wilson et al. 1990b, Pohle et al. 1991, Irlandi 1994, Peterson and Heck 2001).

Although the relationship between increased SAV and decreased predation seems to be ubiquitous, some research has shown increased mortality within SAV habitat. Skilleter (1994) documented decreased survivorship of soft shell clams (*Mya arenaria*) and Baltic clams (*Macoma balthica*) inside a grass bed composed of widgeon grass (*Ruppia maritima*) relative to survivorship in unvegetated habitat. Another scientist reported that populations of *M. arenaria* in Maine and of quahogs or cherrystone clams (*Mercenaria mercenaria*) in North Carolina were reduced within SAV compared to unvegetated areas principally due to increased predation pressure within SAV (Beal 2000). Other research revealed that bay scallops (*Argopecten irradians*) experienced increased predation pressure along the edge of a grass bed when compared to predation within or outside the grass bed (Bologna and Heck 1999).

Location within the grass bed can be important to animal abundance and survivorship as well. Since grass beds rarely have discrete boundaries, the edge of a grass bed is best defined as a zone where SAV density decreases gradually through space. Habitat edges have been shown to sometimes have particularly high species diversity and activity, as the animals from both of the adjacent habitats come in contact and interact with one another (Odum 1959, p. 278). Edge habitats can increase access to food and shelter through the combination of characteristics that are present from both of the adjacent

habitats. Therefore, the influence of SAV on animal abundance may change from inside, to the edges, to outside the grass bed.

Changes in the effects or benefits that SAV habitat has on an organism can also occur in seasonal or annually cyclic patterns. SAV is a biotic habitat, which means that the structure of the habitat itself undergoes changes as the plants mature through their life cycles. In addition, seasonal and annual changes in predator and prey activities modify species interactions and the effect of habitat on animal abundance and survivorship (Holland et al. 1977, Ulanowicz et al. 1982).

One common animal found in SAV habitats of the Chesapeake Bay and its tributaries is the blue crab, *Callinectes sapidus*. Blue crabs are decapod crustaceans of the family Portunidae that inhabit Chesapeake Bay waters from the mouth to tidal fresh waters. They are a swimming crab and grow to a maximum size of about 225 mm (Baker and Mann 1991). Females are highly migratory, moving to the Bay mouth to spawn in early summer. Larvae migrate up the Bay and metamorphose into juveniles, moving into the tributaries and throughout the Bay during the fall. Crabs of all life stages become less active and cease feeding as water temperatures drop below 10º C. During spring and summer, they eat using their two chelipeds to catch, tear, and crush food items that are then moved to the mouthparts for ingestion. They are predators on a variety of foods including juvenile and small adult fish such as mummichogs (Kneib 1982), as well as

polychaetes (Virnstein 1977, 1979), mussels (Seed 1980), and infaunal clams (Virnstein 1977, 1979).

Another group of animals frequently found in Chesapeake Bay waters are infaunal clams. Some of the more common infaunal clam species in the mid to lower Bay include *M. arenaria* (soft shell clam), *M. balthica* (Baltic clam), *Macoma mitchelli*, *Gemma gemma*, (amethyst or gem clam), and *Mulinia lateralis* (little surf or coot clam). Infaunal clams live in shallow waters of the Chesapeake Bay and its tributaries, ranging from the mouth to tidal freshwaters, depending on species. Infaunal clams dig into the sediment using their muscular foot and extend their siphons to the sediment-water interface. These clam species are suspension feeders, taking plankton from the water column, or deposit feeders, taking detritus from the sediment surface, or both. Most of the common mid to lower Chesapeake Bay species have a relatively thin, easily crushed shell. By digging into the sediment, they separate themselves from potential predators.

Research completed in this thesis examined the effect of habitat complexity on survivorship of animal species associated with SAV habitat. Specifically, I investigated whether SAV habitat had an effect on survivorship of infaunal clam species. I used two different approaches to answer this question. In Chapter 2, I describe my field study, in which I measured clam abundance as it related to SAV biomass and location with reference to grass beds in St. Mary's River, Maryland, an estuarine tributary of the Chesapeake Bay. In Chapter 3, I discuss laboratory experiments that I conducted using

artificial SAV, soft-shell clams (*M. arenaria*) as the infaunal clam species, and blue crabs (*C. sapidus*) as the predator. By approaching this investigation both through field surveys and controlled laboratory experiments, I have been able to contribute to the understanding of the relationship between SAV habitat and a group of its inhabitants, infaunal clams.

Chapter 2. Effect of submerged aquatic vegetation as habitat on survivorship of clam species in St. Mary's River, Maryland

INTRODUCTION

Submerged aquatic vegetation (SAV) is one of many habitats found in the shallow waters along the shores of the Chesapeake Bay and its tributaries. It is a complex habitat type and a dynamic system where changes occur both independent of and within cyclical periods such as tides, days, and seasons. Research studies have found that SAV habitat occurs simultaneously with increased abundances of several species of aquatic invertebrates including decapod crustaceans (Heck and Thoman 1984, Orth and van Montfrans 1987, Scott-Denton 1999, Short et al. 2001) and bivalves (Peterson et al. 1984, Peterson 1986, Capehart and Hackney 1989, Irlandi 1994, Irlandi 1997). SAV is important ecologically and economically for several reasons including protection of juvenile fish (Wilson *et al*. 1987, Lubbers et al. 1990) and soft crabs (Wilson *et al*. 1987) from predation, the photosynthetic production of oxygen (Boynton and Heck 1982), utilization of nutrients (Boynton and Heck 1982), and the stabilization of the sediment to reduce erosion from wind-wave effects (Ward *et al*. 1984).

Infaunal clams may benefit from their association with SAV habitat. Infaunal clams burrow into the substrate between grass blades. They extend their incurrent siphon to the sediment-water interface where they take in water for respiration and plankton as suspension feeders or detritus as deposit feeders. Infaunal clam species found in the Chesapeake include *Mya arenaria* (soft-shell clam), *Macoma balthica* (Baltic clam), *Macoma mitchelli*, *Gemma gemma*, (amethyst or gem clam), and *Mulinia lateralis* (little surf or coot clam). With the exception of *M. arenaria*, which grows to 10 cm, these clam species are no larger than 4 cm. All of these species have thin shells that can be crushed fairly easily by predators. Potential benefits provided to clams by SAV habitat include protection from predation (Blundon and Kennedy 1982; Crockett 1989; Irlandi and Peterson 1991; Irlandi 1994, 1997), increased growth rates (Irlandi and Peterson 1991) and reduced exposure to water currents (Irlandi and Peterson 1991).

Predators of infaunal clams in Chesapeake Bay may also benefit from their association with SAV. One of the major predators, *Callinectes sapidus* (blue crab), has been shown repeatedly to exhibit increased abundances within SAV habitat as compared to unvegetated habitat (Heck and Thoman 1982, Heck and Thoman 1984, Anderson and van Heukelem 1995, Rozas and Minello 1998, Scott-Denton 1999). Like their prey, some of the benefits that blue crab and other predators may obtain from SAV are protection from predation (Wilson et al. 1987, Wilson et al. 1990b) and increased growth rates (Perkins-Visser et al. 1996).

One factor that may modify SAV effect on growth and survivorship of animals is their specific location with respect to the grass bed. Grass beds are not habitats with discrete boundaries. Areas inside and outside the grass bed, and the zone at the perimeter of the grass bed, or edge, may vary in their influence on clams. Edges where two habitats come together have been shown to be areas of particularly high species diversity and activity where organisms from both habitats interact (Odum 1959, p. 278). Edges may increase access to food and shelter through their unique mix of characteristics from each of the adjoining habitats (Odum 1959, p. 278). In contrast, areas without structure (e.g., outside the grass bed) may benefit species survival by separating the prey from its predator. Some surveys have shown that survival of *M. arenaria* and *Mercenaria mercenaria* was higher outside the grass bed in the adjacent sand flats than within the grass bed due mainly to lower predation by crabs and other predators who were using the grass bed as their refuge (Beal 2000).

Seasonal or annually cyclic changes within the SAV ecosystem can alter the relationships between species that are found there. Since the actual habitat structure is biotic, it undergoes seasonal changes such as growth and senescence that may influence the animals that live within it. Activity patterns and growth of animal species associated with the SAV community also change seasonally and modify species interactions (Holland et al. 1977, Ulanowicz et al. 1982).

Many factors, including those described here, operate simultaneously and their interactions can substantially change the relationships among animal species, and between animals and the SAV habitat in which they live. The effects of these interactions can alter the mortality, growth, reproduction, survivorship, and overall abundances of the component organisms within the SAV ecosystem.

Identifying factors that drive changes in a system is important for better ecological understanding and management of the aquatic environment. One of the clam species found in Chesapeake Bay SAV habitat is the soft-shell clam, *M. arenaria,* a commercial species fished for human consumption. The usual fishing method for M. arenaria employs a hydraulic escalator dredge. When a dredge is used to harvest clams in SAV habitat, the SAV becomes dislodged and destroyed. Thus, commercial use of one resource, M. arenaria, can cause the destruction of SAV, another important natural resource.

In this field study, I examined clam abundance and SAV biomass at several locations with respect to grass beds. The goal was to determine whether clam abundance varied with habitat complexity or physical location with respect to the surrounding grass bed, and whether that relationship changed between spring and summer. Results can aid in the management of SAV and clams as resources by adding to the

knowledge of the biology, life history, and ecology of these two important Chesapeake Bay resources.

METHODS AND MATERIALS

Ninety-six sample cores were taken in three *Ruppia maritima* beds in the St. Mary's River, Maryland, USA during summer 2000, spring 2001, and summer 2001. Spring sampling dates were chosen to be times several weeks after water temperature had increased above 10º C, so that the spring clam spawning event had occurred and clam larvae had settled out of the water column and had grown large enough to be retained by the sampling bag mesh. Summer sampling dates were chosen to coincide with the maximum water temperatures for the season. Sampling dates for each site and replicate numbers can be seen in Tables 1 and 2. Figures 1a and 1b contain maps showing the sampling sites.

Table 1. List of sites and dates for field sampling events.

Site	Position on River	Summer 2000	Spring 2001	Summer 2001
H	Above Chancellors Pt	7/04/00	--	--
G	Below Chancellors Pt	--	4/27/01	8/01/01
X	Below Windmill Pt	--	5/08/01	8/07/01

Table 2. Number of replicate samples for each location at each site and date for field sampling events.

		Location			
Site	**Date**	**Inside**	**Edge**	**Outside**	**Outside 2**
H	7/04/00	6	6	3	0

G	4/27/01	6	6	4	4
G	8/01/01	6	5	4	4
X	5/08/01	6	5	2	4
X	8/07/01	6	6	4	4

Cores were taken within SAV beds, along the boundary between the SAV and the adjacent sand flat, in the adjacent sand flat outside of the grass bed, and in the sand flat further (~5m) from the grass bed. These areas will be referred to as *locations*, specifically as *inside*, *edge*, *outside*, and *outside 2*, respectively. The approximate locations (in reference to the grass bed) are illustrated in Figure 2; the exact position of each core was determined using a random number of paces (between 0 and 9) from the reference positions given in Figure 2. Outside and outside 2 samples were collected approximately 2 m and 5 m from the edge of the grass bed, respectively. Outside 2 locations were used to ensure that samples were indeed collected outside the grass bed, as the edge of a grass bed is not a discrete line and is sometimes difficult to determine.

Cores, measuring approximately 30 cm in depth and 670 cm^2 in surface area (diameter of 29.2 cm), were collected utilizing a suction sampler and sieved in-line to 1.5 mm (Lucy 1976, Blundon and Kennedy 1982, Orth and van Montfrans 1987, Hines *et al*. 1990, Eggleston *et al*. 1992). Samples were then taken to the laboratory where SAV and all bivalves live at the time of sampling were separated from sediment for analysis. I categorized clams as "alive" if they contained tissue inside the shells that was not autolyzed. SAV was dried at 100º C for 48 h to a constant weight (Capehart and Hackney 1989) and dry mass was measured and recorded. Bivalves were identified to

species. Anteroposterior valve length was measured and recorded for each individual. Total densities of each species of clam were enumerated for each core.

Figure 1a. Map of sampling sites along the St. Mary's River, Maryland.

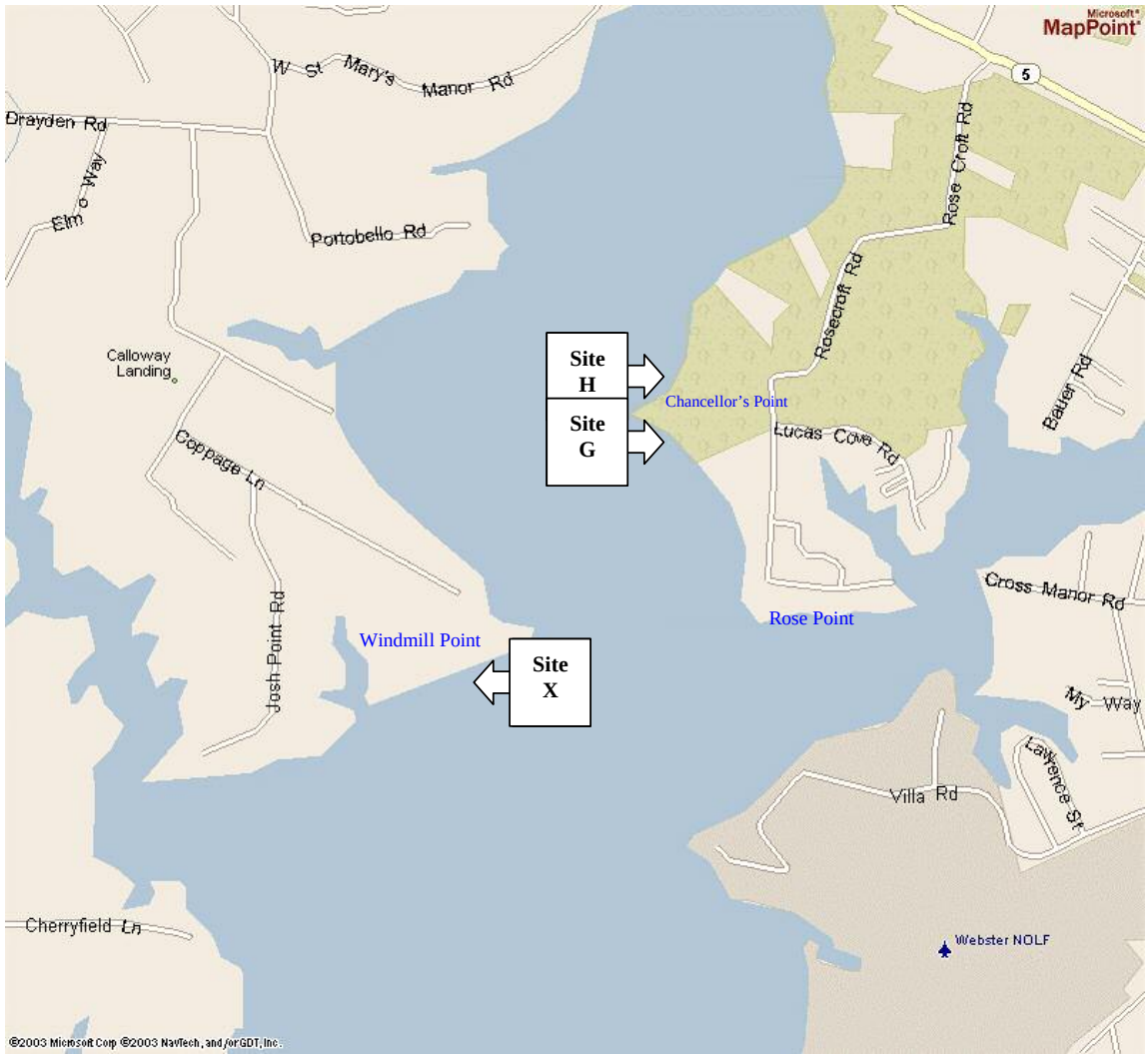

Figure 1b. Map of sampling sites G, H, and X along the eastern and western shores of the St. Mary's River near Windmill & Chancellor's Points.

Data collected from these samples enabled me to examine the effect of both SAV biomass and location for clam abundance. I was also able to investigate seasonal changes in these effects.

Hypotheses

Null Hypothesis: Location with reference to the grass bed (inside, along the edge of the grass bed, or outside the grass bed) and SAV biomass have no affect on clam abundance.

Alternative Hypothesis: Clam abundance will vary with location (inside, along the edge of a grass bed, or outside the grass bed) and SAV biomass. Clam abundance will be highest inside, lowest outside, and at an intermediate level along the edge of the grass bed. There will be a positive relationship between SAV biomass and clam abundance, because predation on clams will be highest in areas without SAV.

Due to seasonal patterns of growth, reproduction, and senescence of SAV, as well as growth of clams and increases and decreases in predator activity, the relationship between clams and their habitat can potentially change with season. I therefore examined the effects of location and SAV density on clam abundance separately during spring and summer, so that site H (which was only sampled in the summer) could be included in the summer analyses. I also examined whether effects of location and SAV varied between spring and summer using an analysis of the two sites (G and X) that were sampled in both seasons.

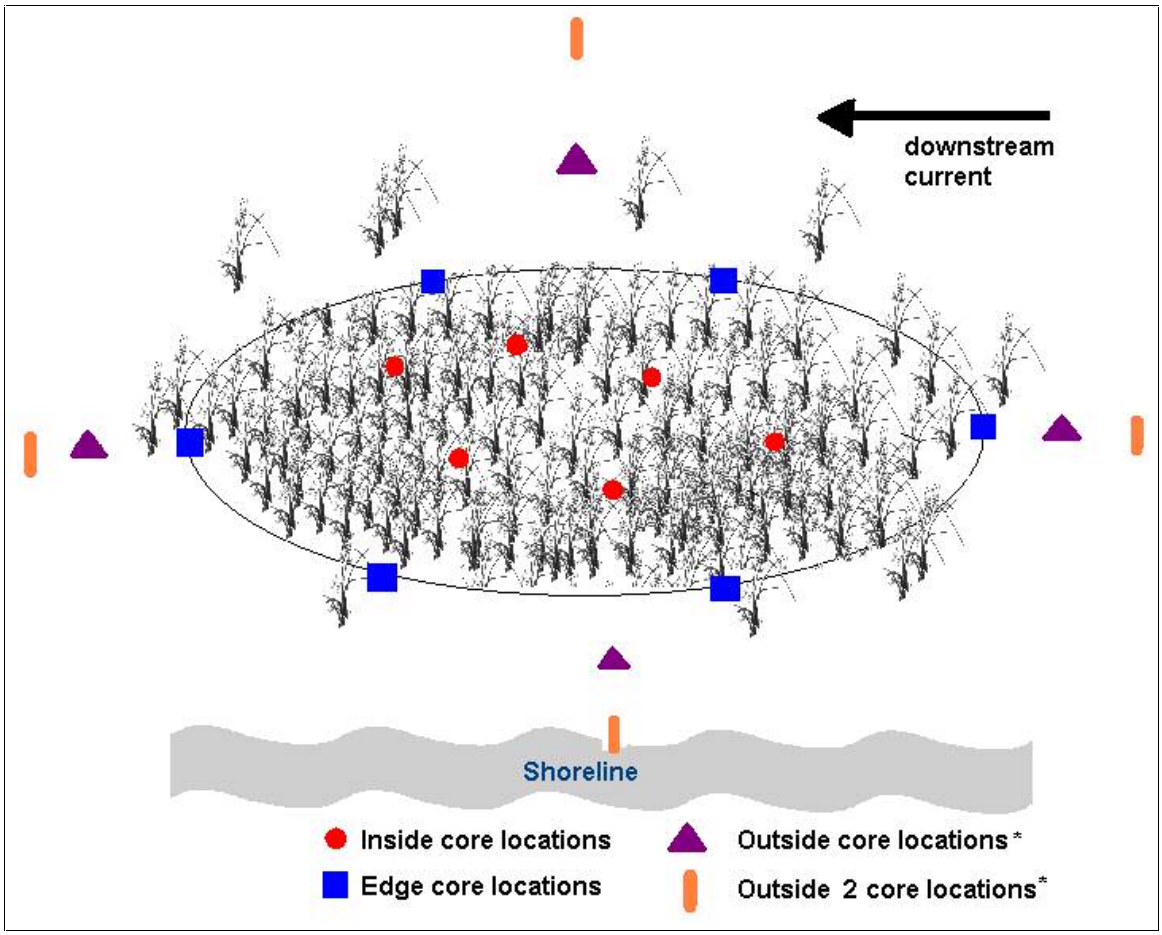

Figure 2. Schematic of reference locations of the sample cores. Actual locations varied from this schematic and were randomized. *The schematic is not to scale; the outside core and outside 2 sampling locations are 2m and 5m away from the edge of the grass bed.

Spring sampling dates

The effect of location and SAV biomass on clam abundance during spring was investigated for the samples taken in the spring of 2001 at sites G and X. This analysis was blocked by site.

For the spring samples, I expected the data to support the null hypothesis because clams spawn in the late fall after predator activity has decreased and these samples were taken prior to the height of summer predator activity. Therefore, I did not expect clam abundance to be correlated with SAV biomass or vary among locations.

Summer sampling dates

The effect of location and SAV biomass on clam abundance during summer was investigated for samples taken in the summer of 2000 at site H and the summer of 2001 at sites G and X. All the sites were similar in structure and were close to one another. The outside 2 location was not added to the sampling protocol until 2001. Therefore, site H was not sampled at the outside 2 location. This analysis was blocked by site.

I predicted that clam abundance would be lowest in the outside and outside 2 locations where there was virtually no protective cover by the grass bed and highest in the inside location which had the highest SAV density because predators would be active during the summer. For the same reason, I predicted a positive relationship between SAV biomass and clam abundance during summer.

Comparison of spring samples to summer samples.

Data were examined to see if seasonal variation in the environment could lead to a different affect of location and SAV on clam abundance during spring and summer.

Null Hypothesis: Season (spring, summer) has no effect on clam abundance. The relationship between clam abundance, location, and SAV will be the same in spring and summer.

Alternative Hypothesis and Rationale: Season has a significant effect on clam abundance. Clam abundance at any particular location or SAV biomass is higher in the spring than in summer. This difference occurs due to predation by animals that become much more active in between the spring and summer sampling events. I expect the season*SAV and/or season*location interactions to be significant showing that SAV biomass and/or the inside location of the grass bed to be more predictive of clam abundance in the summer than in the spring.

Crab abundance

Crab pots were set out in the grass beds to obtain information about the abundance of predators in the area at the time of sampling. Six peeler crab pots (2.5 cm mesh) were set out in sites H, G, and X in the spring and summer of 2001 within three days of sampling events at each of these sites. The pots were baited with fish (Atlantic menhaden,

Brevoortia tyrannus). Three crab pots were haphazardly placed inside the grass bed and three pots were haphazardly placed 2 to 5 m away from the edge of the SAV, outside the grass bed. The pots were left for 48 hours at which point they were collected and the crabs inside were sexed, measured, and released.

Statistical Analyses

For separate analyses of spring and summer samples, I used a randomized complete block design (RCBD) analysis of variance (ANOVA) to determine if clam abundance varied with SAV biomass or location or the interaction between SAV and location. Site was incorporated as a random blocking factor. If SAV was found to be significant, a second RCBD analysis was also carried out to examine the relationship between clam abundance and location without considering SAV directly. This second analysis was used to see if differences in clam abundance among locations were attributed to variation in SAV biomass in the original ANOVA.

These analyses were conducted for all clam species combined and for the most abundant clams in the field samples, *Macoma* spp. (*M. balthica* and *M. mitchelli*). The two *Macoma* species were combined in these analyses because they are similar in adult size, life histories, and burrowing depths, and are both deposit feeders.

For the spring to summer comparison the same analysis as described above was used with the additional factor of season added to the model (i.e., clam abundance = SAV biomass + location + season + SAV*location + SAV*season + location*season + SAV*location*season). Site was used as a random blocking factor.

The number of replicates varied among locations with lower replication in the outside and outside 2 locations. I therefore reran the same analyses as described above on the data with the outside and outside 2 locations combined in order to increase sample size for this 'combined outside' location, and reduce the number of location treatments. The analyses using three locations instead of four showed no differences in significance compared to those using four locations, and are therefore not presented.

The statistical software utilized for all data analyses was SAS Version 8.0. All data were examined and passed tests for normality, homogeneity of residual variances, and normality of residuals, except where noted. Inverse (1/x) and $\log_{10}$-transformations were used where noted to make data meet anova assumptions. The PROC MIXED procedure was utilized for all ANOVAs.

RESULTS

Overall sampling

SAV biomass in individual samples ranged from 0 to 441 g/m^2, with a mean and standard error of 62.5 ± 10.0 g/m^2. A randomized complete block design (RCBD) analysis of variance (ANOVA) of inverse-transformed SAV biomass across all dates and sites with site as a blocking factor revealed that locations had significantly different SAV biomasses ($F = 27.08$, $p < 0.0001$, Fig. 3). SAV biomass decreased across inside, edge, outside, and outside 2 locations. An aposteriori pairwise comparison test using the Tukey-Kramer adjustment for unequal sample sizes indicated that the inside location was significantly different from the edge, outside, and outside 2 locations and that the edge location was different than the outside 2 location. The SAV biomass at the inside location was more than twice as large as that of the edge location and more than eight times larger than that of the outside and outside 2 locations. Site G contained a mean of 53.4 ± 12.9 g/m^2 of SAV biomass (spring and summer samples combined); Site H had 20.5 ± 5.36 g/m^2 (summer samples only), and Site X had 89.4 ± 19.6 g/m^2 (spring and summer samples combined).

There were between 0 and 80 clams of five species per sample (0 to 1190 clams/m^2), with a mean of 82.8 ± 16.9 clams/m^2. *M. balthica* was by far the most common clam species found, comprising 44 percent of the total number of clams. Following this, *M. mitchelli* was the most common clam species at 31 percent of the total. Together these two

Macoma species comprised 75 percent of the clam abundance seen in the samples. Less abundant clam species were *M. arenaria* (12%), *G. gemma* (10%), and *M. lateralis* (1%). The mean numbers of *M. balthica* and *M. mitchelli* were 36.6 ± 11.6 and 25.5 ± 4.03 per m^2 respectively, with a range of 0 to 836 clams/m^2 for *M. balthica* and a range of 0 to 179 clams/m^2 for *M. mitchelli*. All clam species combined ranged from 1.06 mm to 86.0 mm in length and averaged 8.06 ± 0.356 mm. Mean lengths ranged from 1.87 ± 0.0630 mm for *G. gemma*, the smallest clam sampled, to 18.9 ± 1.86 mm for *M. arenaria*.

The mean number of clams/m^2 found at each site was: 94.9 ± 36.9 at Site G, 92.6 ± 12.2 at Site H, and 66.1 ± 14.4 for Site X. The mean number of clams/m^2 found at each location across all sites were: inside = 134 ± 41.2, edge = 79.4 ± 29.0, outside = 40.5 ± 13.4, and outside 2 = 38.2 ± 14.0.

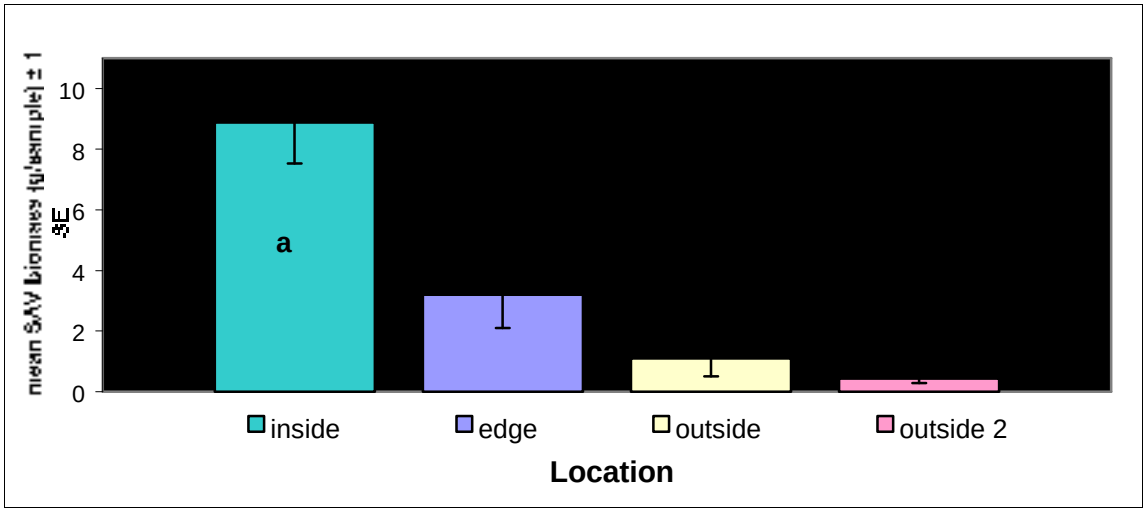

Figure 3. Mean SAV biomass by location across all samples. Different letters represent significant differences among locations.

Spring sampling dates

In the spring samples, SAV biomass ranged from 0 to 441 g/m^2 with a mean of 75.5 ± 19.0 g. Site G had a mean of 54.9 ± 19.6 g/m^2 and Site X had 99.9 ± 34.0 g/m^2. Mean SAV biomass averaged across sites was: inside = 167 ± 33.0 g/m^2, edge = 66.1 ± 29.3 g/m^2, outside = 4.64 ± 1.69 g/m^2, and outside 2 = 4.51 ± 2.78 g/m^2. An RCBD AVOVA of inverse-transformed SAV biomass indicated that locations had significantly different SAV biomasses during spring ($F = 23.62$, $p < 0.0001$). An aposteriori pairwise comparison test using the Tukey-Kramer adjustment for unequal sample sizes indicated that the following pairs of locations were different: inside and edge, inside and outside, inside and outside 2, edge and outside 2.

Clam abundance for all species combined ranged from 0 to 1190 clams/m^2 and averaged 122 ± 38.4 clams/m^2. The mean number of clams/m^2 found at each site was: 165 ± 68.7 at Site G and 71.0 ± 18.4 at Site X. The mean number of clams found at each location averaged across sites followed the same trend as SAV biomass. Clam densities at the inside location were approximately three times larger than those at the outside and outside 2 locations (Fig. 4). Edge location densities were intermediate between inside and outside/ outside 2 densities, at about half the density of the inside location. There were 91.5 ± 32.5 *Macoma* spp. clams/m^2.

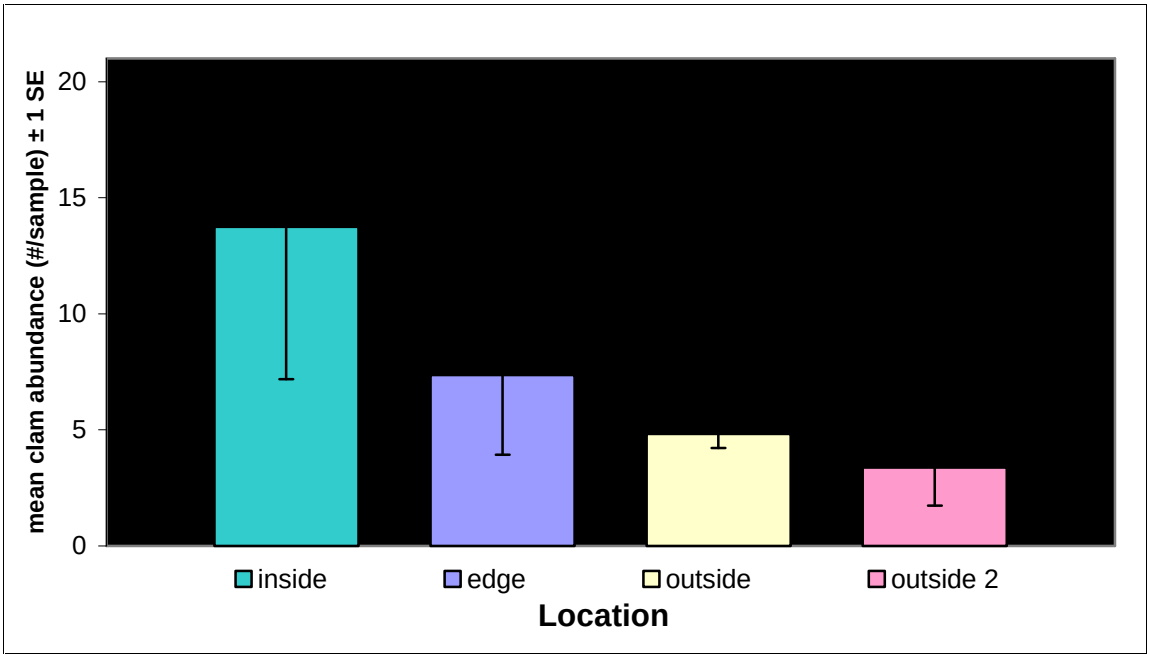

Figure 4. Mean clam abundance averaged across spring samples by location.

An RCBD ANOVA on $\log_{10}$-transformed clam density data indicated that neither SAV biomass ($F = 1.59$, $p = 0.216$) nor location significantly affected clam abundance during spring ($F = 0.44$, $p = 0.726$; Fig. 5). Similarly, an RCBD ANOVA on $\log_{10}$-transformed clam density and SAV biomass data of *Macoma* spp. clams indicated that neither SAV biomass ($F = 1.71$, $p = 0.201$) nor location ($F = 0.30$, $p = 0.822$) significantly influenced *Macoma* spp. abundance during the spring (Fig. 6).

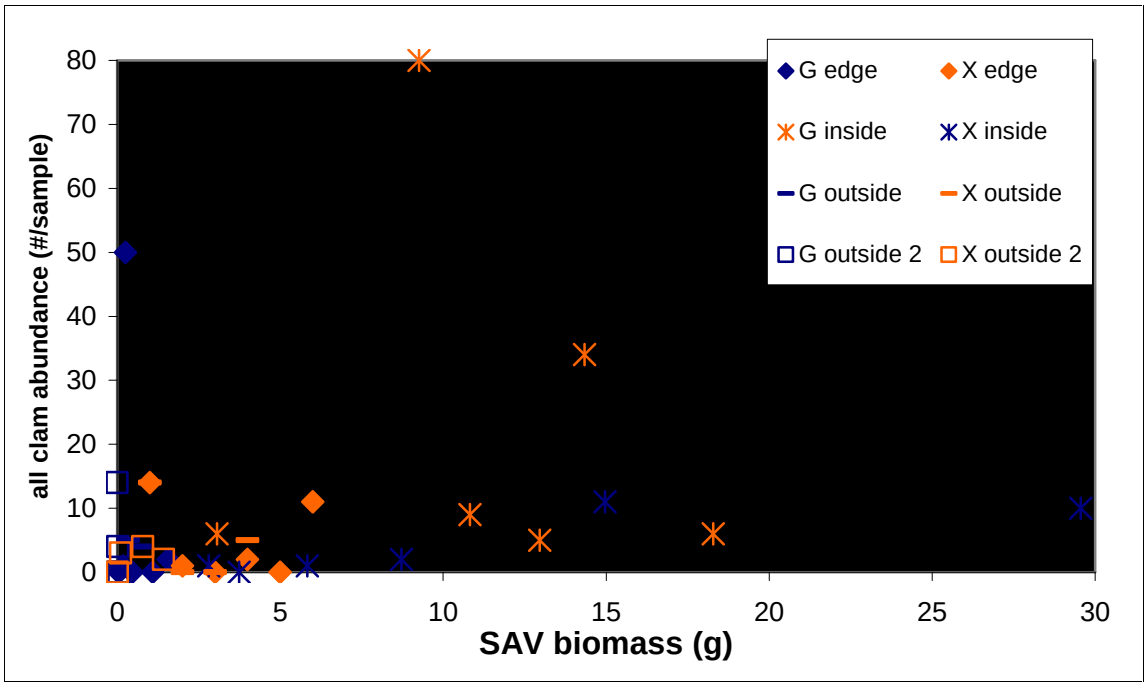

Figure 5. SAV biomass versus all clam abundance for spring samples.

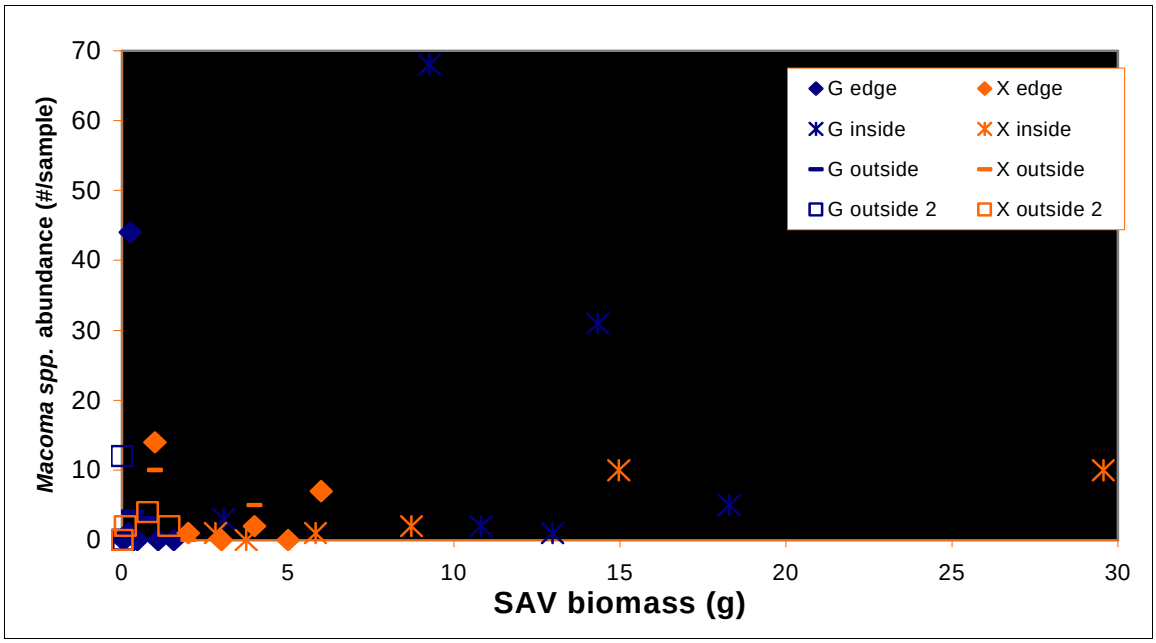

Figure 6. SAV biomass versus Macoma spp. abundance for spring samples.

Summer sampling dates

In the summer samples, SAV biomass ranged across all samples from 0 to 406 g/m^2 with a mean of 53.7 ± 10.7 g/m^2. Mean SAV biomass at Site G was 51.8 ± 12.0 g/m^2; Site H averaged 20.5 ± 5.36 g/m^2 and Site X averaged 80.5 ± 16.6 g/m^2. The SAV biomass averaged across the three sites by location was: inside = 109 ± 24.8 g/m^2, edge = 35.8 ± 8.60 g/m^2, outside = 23.0 ± 10.8 g/m^2, and outside 2 = 8.31 ± 2.15 g/m^2. An RCBD AVOVA of inverse-transformed SAV biomass indicated that locations had significantly different SAV biomasses ($F = 8.93$, $p < 0.0001$). An aposteriori pairwise comparison test using the Tukey-Kramer adjustment for unequal sample sizes indicated that the inside location had a different SAV biomass than the outside and outside 2 locations.

Clam abundance in the summer samples from all sites ranged from 0 to 313 clams/m^2 with a mean of 56.1 ± 9.91 clams/m^2. Clam abundance was: 21.2 ± 5.82 clams/m^2 at Site G, 92.5 ± 12.2 clams/m^2 at Site H, and 61.9 ± 16.1 clams/m^2 at Site X. There was an average of 35.7 ± 6.18 *Macoma* spp. clams/m^2.

An RCBD ANOVA on $\log_{10}$-transformed clam density data indicated that SAV biomass ($F = 5.70$, $p = 0.021$, Fig. 7) significantly influenced clam abundance in the summer samples. Location within the grass bed was not significant ($F = 1.33$, $p = 0.277$). An RCBD ANOVA using $\log_{10}$-transformed clam density data that considered only the effect of location on clam abundance (without SAV biomass) indicated that location was significant ($F = 3.47$, $p = 0.023$). Clam abundance decreased in locations further from the interior of the grass bed (Fig. 8). An aposteriori pairwise comparison test using the Tukey-Kramer adjustment for unequal sample sizes indicated that the inside and the outside locations had significantly different clam abundances.

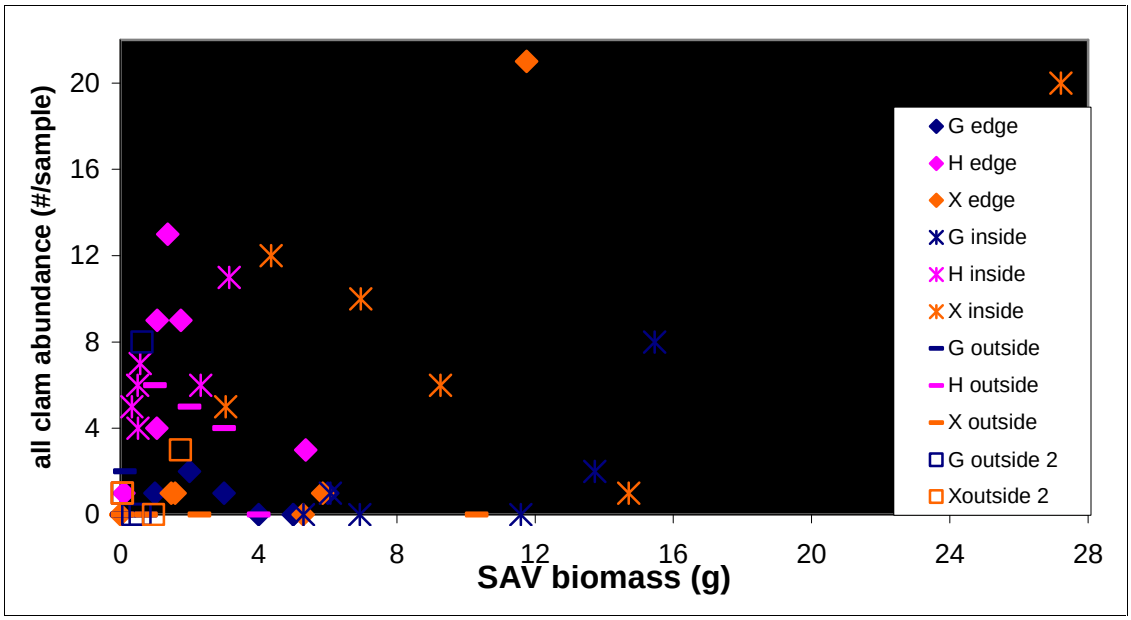

Figure 7. SAV biomass versus all clam abundance for summer samples.

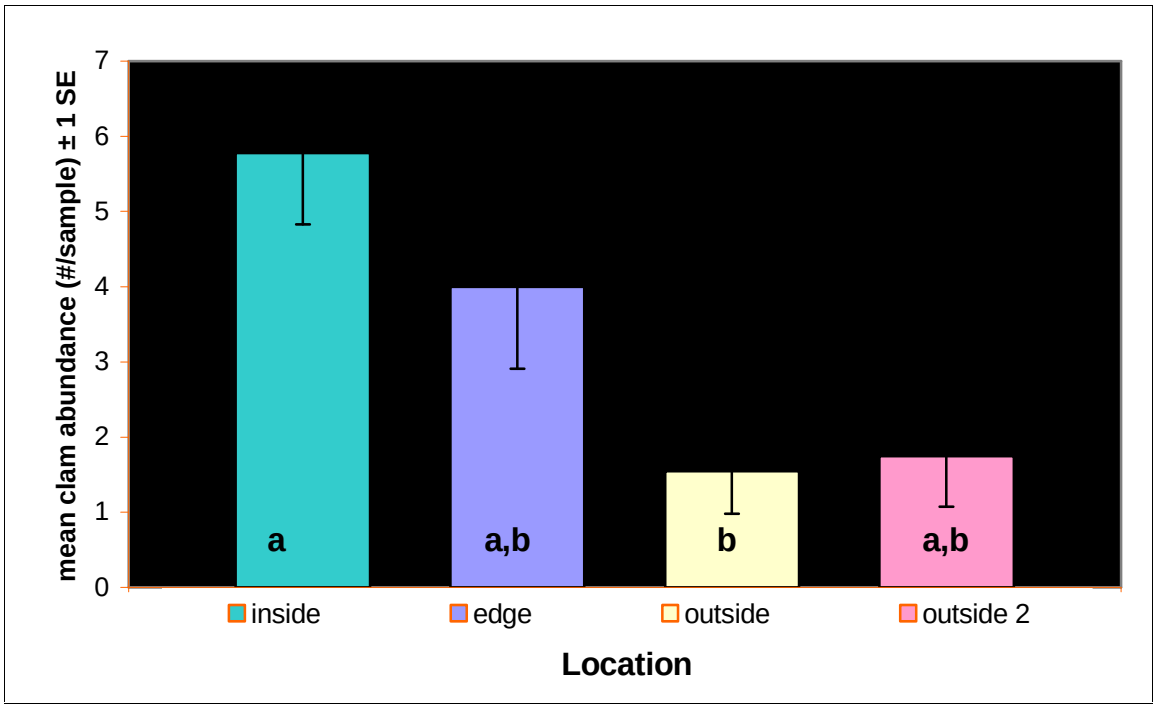

Figure 8. Mean clam abundance across all summer samples by location. Different letters represent significant differences among locations.

Results for *Macoma* spp. were similar to those for all clam species combined. An RCBD ANOVA on $\log_{10}$-transformed clam density data of *Macoma* spp. clams indicated that SAV biomass was significant ($F = 9.80$, $p = 0.003$) but that location was not significant ($F = 1.00$, $p = 0.401$, Fig. 9). Unlike the results for all clam species combined, however, an RCBD ANOVA on $\log_{10}$-transformed *Macoma* spp. density data testing the effects of location (without inclusion of the potential SAV biomass effect) indicated that location was not a significant factor in *Macoma* spp. abundance ($F = 1.12$, $p = 0.349$).

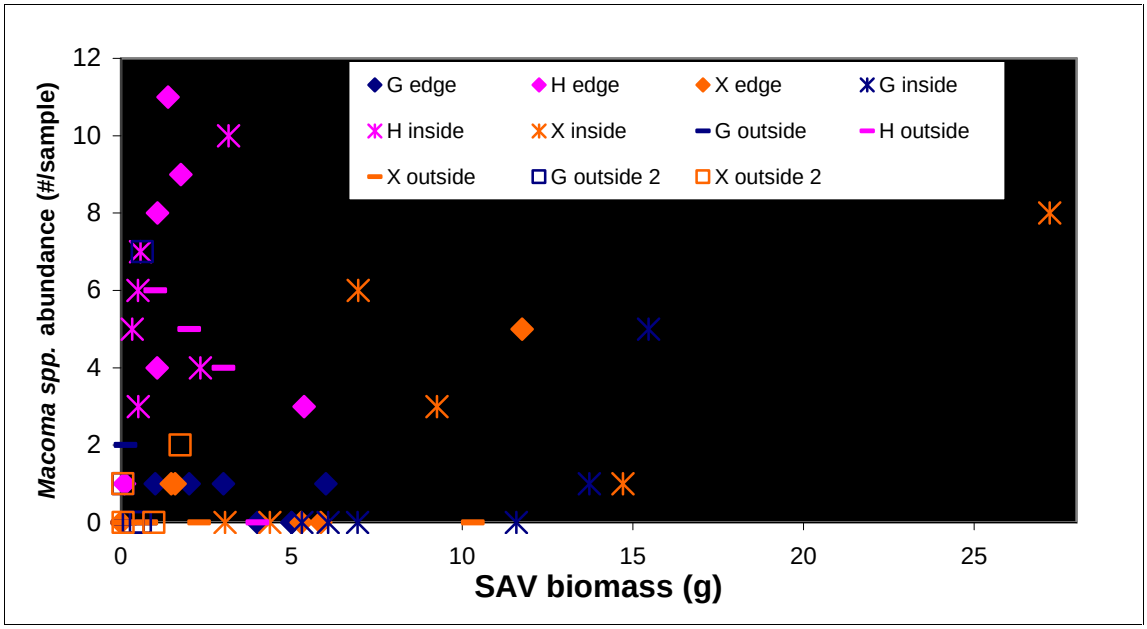

Figure 9. SAV biomass versus clam abundance for *Macoma* spp. in summer samples.

Comparison of spring samples to summer samples

This analysis included the spring and summer sampling dates for Site G and Site X. An RCBD ANOVA on $\log_{10}$-transformed clam density and SAV biomass data indicated that SAV biomass significantly influenced clam abundances ($F = 4.73$, $p = 0.033$, Fig. 10). As SAV biomass increased, the number of clams found in the sample also increased. Location was not significant in this analysis ($F = 0.22$, $p = 0.880$). Season significantly affected clam abundance in that clams were less abundant in the summer than in the spring ($F = 7.92$, $p = 0.006$, Fig. 11). None of the interaction terms in this analysis were significant.

An RCBD ANOVA using inverse-transformed clam density data without SAV biomass as a factor indicated that location ($F = 3.01$, $p = 0.036$) and season ($F = 5.38$; $p = 0.023$) both significantly affected clam abundance. Figure 12 provides the means and standard errors for clam abundance in each location by season category.

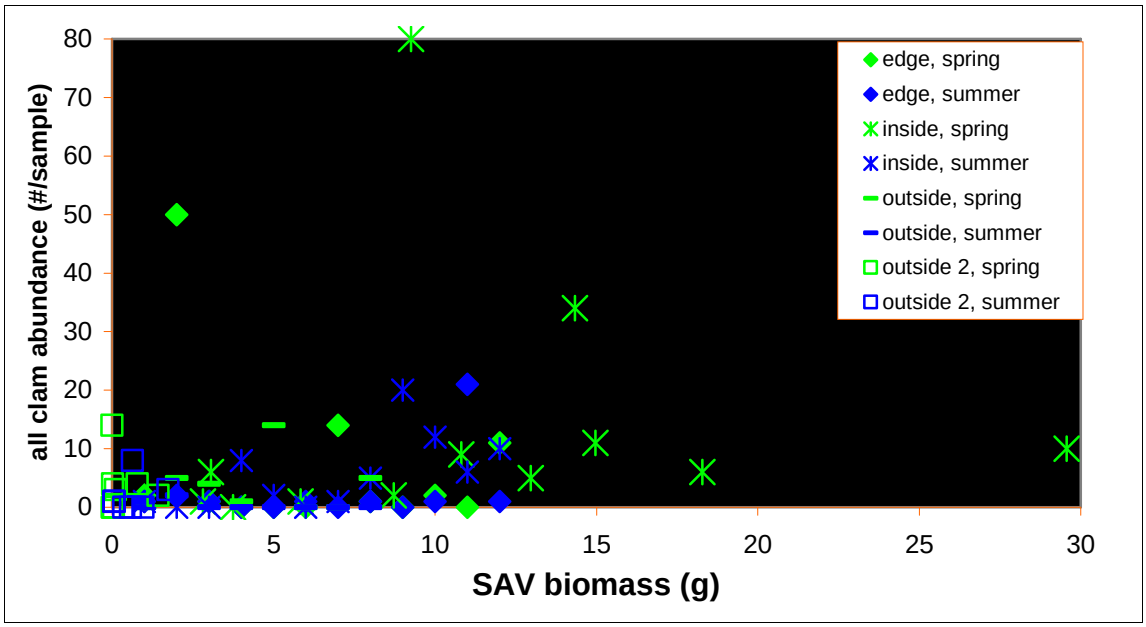

Figure 10. SAV biomass versus all clam abundance for the spring and summer samples by location and season.

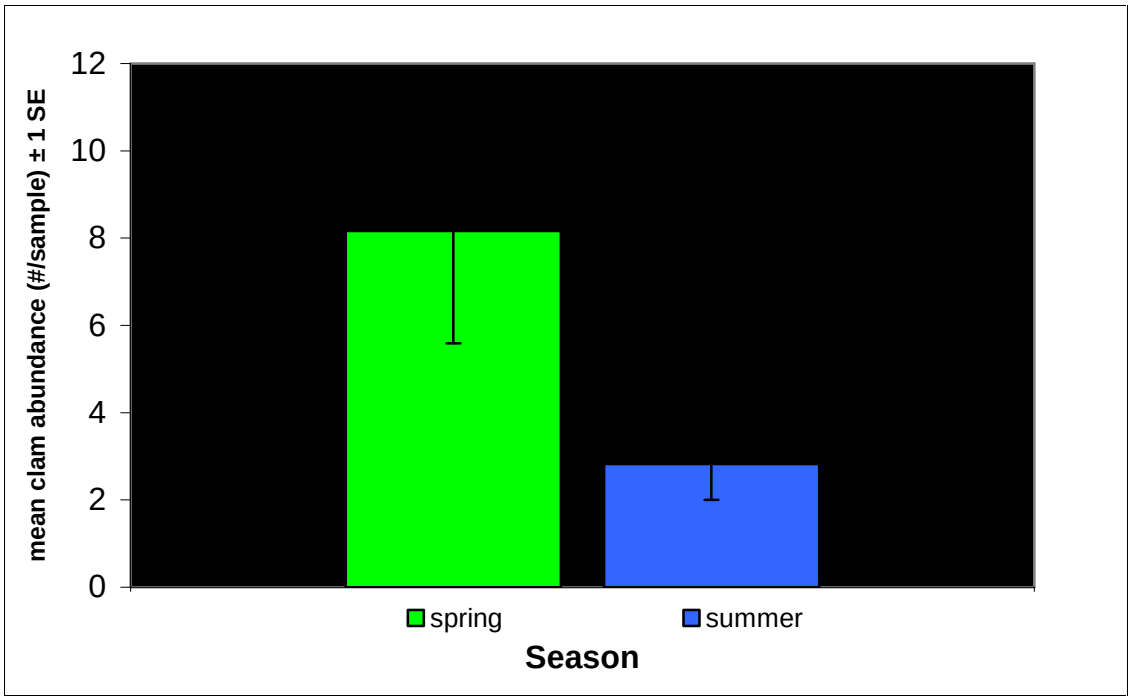

Figure 11. Mean clam abundance across all sites and locations by season.

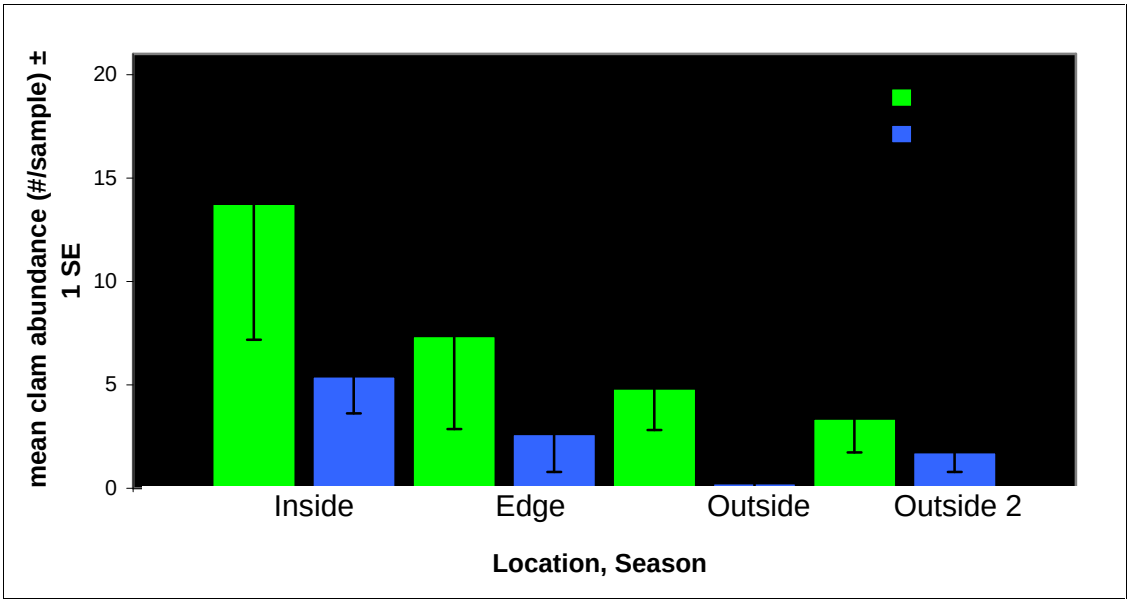

Figure 12. Mean clam abundance for each location by season across all spring and summer samples.

An RCBD ANOVA on inverse-transformed (1/x) clam density data of only *Macoma* spp. clams indicated that SAV biomass was significant ($F = 7.32$, $p = 0.009$, Fig. 13) but location was not ($F = 0.10$, $p = 0.962$). As SAV biomass increased, the abundance of *Macoma* spp. also increased. In addition, season had a significant effect on *Macoma* spp. abundance (spring = 98.8 ± 33.4 clams/m^2, summer = 18.4 ± 5.07 clams/m^2; $F = 6.91$, $p = 0.011$). None of the interaction terms were significant in this analysis. An RCBD ANOVA on inverse-transformed *Macoma* spp. density conducted to examine the effects of location regardless of SAV biomass effect also indicated that location was not a significant factor in clam abundance ($F = 1.43$, $p = 0.242$). Season, however, remained significant in this analysis ($F = 6.94$, $p = 0.010$), with lower clam abundance in the summer than in the spring.

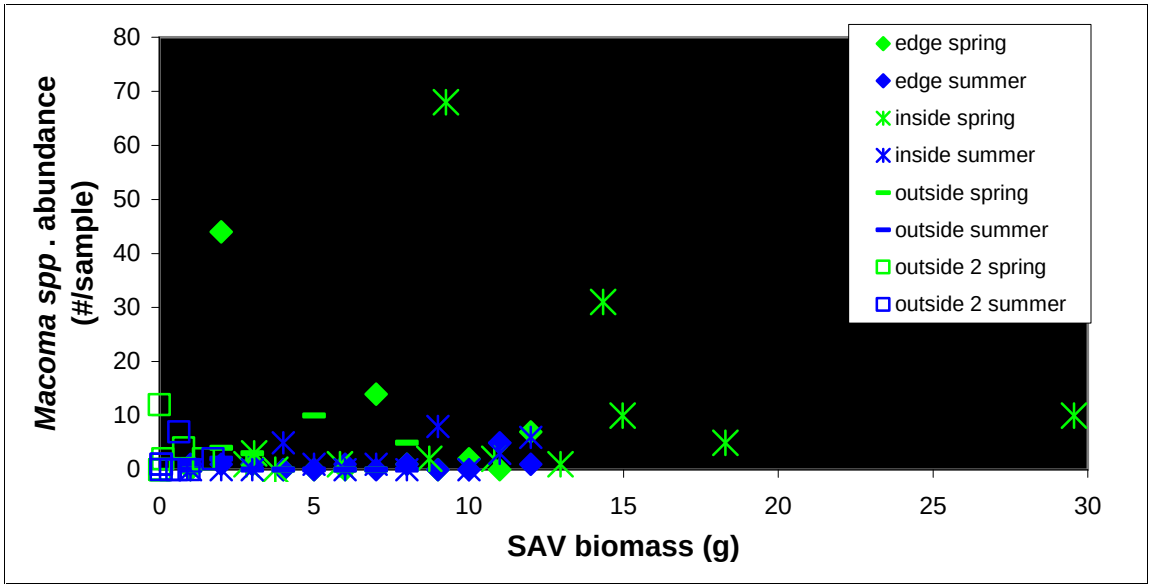

Figure 13. SAV biomass versus *Macoma* spp. clam abundance for spring to summer comparison by location and season.

Crab abundance

A total of 24 crab pots were baited and collected during this part of the study. The number of crabs caught per pot ranged from 0 to 17, with a mean and standard error of 5.58 ± 0.84 crabs per pot. An RCBD analysis of variance (ANOVA) of crab abundance in pots across all dates and sites with site as a blocking factor revealed that locations (inside versus outside) had significantly different numbers of crabs ($F = 5.20$, $p = 0.0337$, Fig. 14). There were significantly fewer crabs caught inside the grass bed than outside the grass bed. Season ($F = 0.03$, $p = 0.859$) and the interaction between location and season ($F = 0.61$, $p = 0.444$) were not significant.

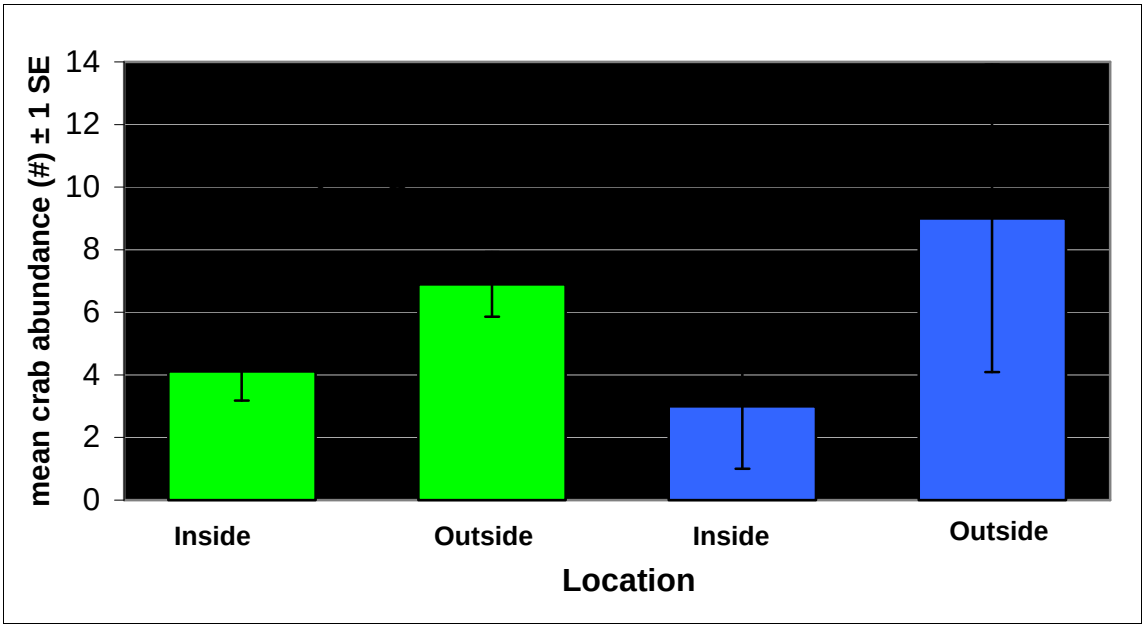

Figure 14. Mean crab abundance for pots by location and season.

DISCUSSION

Spring sampling dates

The analysis of spring samples both for all clams and for *Macoma* spp. indicated that neither SAV biomass nor location significantly influenced clam abundance. Although several complex ecological scenarios could be causing this relationship, one plausible explanation is that larval settlement is similar in all locations and predator activity had not yet increased to a level sufficient to alter the settlement pattern. Both *M. arenaria* (Pfitzenmeyer 1962) and *M. balthica* (Holland et al. 1977) have been shown to recruit heavily in the winter months. *M. arenaria*, *M. balthica*, and *M. mitchelli* are planktonic

spawners whose larvae remain in the water column for approximately two weeks before metamorphosing and settling to the bottom. Since they are planktonic and cannot swim against currents (Chia et al. 1984, Roegner 2000), it is possible that larvae settle at similar densities at all locations with respect to the grass bed. Predation pressure on these species is fairly low in the winter (Brousseau 1978, Holland et al. 1977, Holland et al. 1980) and so the changes to clam settlement distribution resulting from predation might not be significant. A result could be abundances similar to what was found in this survey; clam distribution that was not affected by SAV biomass nor by location with respect to the grass bed in spring.

However, the possibility that nonsignificant statistical findings were the result of relatively low sample size and high variability among spring replicate samples cannot be ruled out. The pattern of greater clam abundances inside the grass bed, less in the edge location, and even less outside the grass bed is found in both the spring and the summer samples. In comparison to summer, the pattern in spring is weaker and more variable. However, some studies have shown that invertebrate larvae do not settle with equal distribution across SAV habitats (Eckman 1983) and that some postlarvae can resuspend into the water column utilizing water currents to move to more favorable habitat (Huxhaum and Richards 2003). Combining differential clam settlement with lower predation pressure in spring might explain the clam abundances seen in the spring samples.

Summer sampling dates

Analyses of the summer samples indicated that SAV biomass was a significant factor in the abundance of both the collective clam assemblage and the two species of *Macoma*. Numerous studies have shown an increased abundance of aquatic invertebrates in conjunction with SAV (Peterson 1982, Heck and Thoman 1984, Peterson et al. 1984, Peterson 1986, Orth and van Montfrans 1987, Capehart and Hackney 1989, Rozas and Minello 1998, Scott-Denton 1999, Peterson 2000, Castellanos and Rozas 2001, Short et al. 2001). Additionally, several studies have shown that aquatic invertebrates obtain protection from predation by locating within submerged vegetation in shallow estuarine habitats (Heck and Thoman 1982; Wilson et al. 1987; Wilson et al. 1990a; Wilson et al. 1990b, Pohle et al. 1991, Irlandi 1994, Peterson and Heck 2001). In the summer, predation pressure on infaunal bivalves is extremely high (Holland et al. 1980). I propose that the additional protection provided by SAV under increased predation pressure is probably the major reason that the distributions of clams differ across the range of SAV biomass. This thick visual and physical barrier hinders the ability of crabs (Heck and Orth 1980a, Kneib 1984) and finfish (Savino and Stein 1982, Graham et al. 1998) to prey on clams. My laboratory experiments (Chapter 3) also support this conclusion by suggesting that SAV presence significantly reduces blue crab predation on M. arenaria. The proportion of clams consumed in unvegetated

habitat was 1.7 times higher than the consumption in the presence of artificial SAV.

This conclusion is, however, contrary to some published studies reporting that M. arenaria (Skilleter 1994, Beal 2000) and M. balthica (Skilleter 1994) mortality is increased within the SAV habitat due to predation. Skilleter (1994) found higher mortality of *M. arenaria* and *M. balthica* within a bed of *R. maritima* compared to bare sediment. He suggested that rhizomes of the SAV could prevent the clams from digging as far into the sediment as they could in open sand flats, making them more susceptible to predation by crabs.

Analysis of the entire clam assemblage in my summer samples indicated that clam abundance varied significantly among locations if SAV biomass was removed as a factor of the analysis. The analysis of SAV biomass by location also showed that SAV biomass was significantly different among locations. Thus, differences in SAV density among locations likely affect differences among locations in clam abundance rather than any inherent property of location, per se.

Comparison of spring samples to summer samples

In the analyses comparing spring to summer samples, season was a significant factor in all analyses for both the entire group of clam species as well as the two species of

Macoma. SAV was also significant in each of these analyses. These results indicate that clam abundance is decreased both in the summer compared to the spring as well as in areas where SAV biomass is lower.

Both my study, which included five clam species, and an earlier study of *M. balthica* and *M. arenaria* at deeper sites (Holland et al. 1977) indicate that clam abundances in Chesapeake Bay show strong seasonal variability. The population abundance cycle climaxes in the spring, declines to minimal (sometimes undetectable) levels in the summer, and after a late-fall spawning event, increases during the winter. At the 9 m depth studies by Holland et al. (1977), the seasonal cycle was caused by hypoxic conditions at the sediment-water interface during the summer. In the shallow waters of my study sites, the cycle is most likely being caused by high predation pressure in the summer (Holland et al. 1980) and a large recruitment in the late fall (Pfitzenmeyer 1962, Holland et al. 1980).

Persistence of these species despite high summer mortality is facilitated by their high reproductive capability. A single reproductive female M. arenaria can produce three million larvae annually (Belding 1930). Of these larvae, only 40 individuals must settle and metamorphose into spat in order to continue to replace the adult population (Ayers 1956).

In the analysis of the entire clam group abundance that examines location within the grass bed in the absence of any SAV biomass effects, location is significant. As in summer, this finding likely reflects the differences among locations in their SAV biomasses. Although in the spring analysis, location was not a significant factor, the increase in replications in this analysis (n = 76) over that of the spring (n = 37) may be the reason that location was significant in this analysis.

A confounding factor to these analyses would be present if recruitment occurred between the spring and summer sampling dates. The study was designed to avoid this problem by sampling after the spring spawning event and prior to the fall spawning event. Therefore, the differences between the abundances seen in the spring and the fall cannot be attributed to new settlement.

Also, it is entirely possible that the differences between the clam abundances recorded in the spring and summer were caused by the greater length of time that predators had to prey on clams by the summer sampling versus the spring sampling, since no recruitment occurred between sampling dates. However, I believe that the documented predation levels seen in the summer as compared to the spring in Chesapeake Bay far outweigh the possibility that time is the only factor at work here.

Crab abundance

In the crab pot study I caught more crabs outside the grass bed than inside in both seasons. This result is contradictory to most research on crab abundance and SAV that indicates that crab abundance is increased within SAV (Heck and Thoman 1982, Heck and Thoman 1984, Anderson and van Heukelem 1995, Rozas and Minello 1998, Scott-Denton 1999). However, most studies on crab abundance have used collecting methods such as nets to determine abundance. Since I used baited pots, the crabs that I caught were those that were active and searching for food. Both my laboratory experiments and the summer sampling suggest that crabs prefer to eat in unvegetated habitat. In addition, most crab abundance studies are done during the day, but my crab pots were left in place for 48 hours, allowing both day and night activity by the crabs to occur while the pots were in place. Studies have shown that blue crabs are more nocturnal (Hoese et al. 1968, Livingston 1976) and some indicated that blue crabs feed at night and avoid predators during the day (Darnell 1958). Therefore, my findings from the crab pots may indicate that more blue crabs were caught outside the SAV because they traveled outside the grass bed to feed at night and were attracted by the bait in the pots.

Although the discussion of clam predation focuses on blue crabs because they are a major predator, many other animals associated with SAV habitat prey on clams as well. These predators include mud crabs (*Panopeus herbstii*) (Whetstone and Eversole 1978), cownose rays (*Rhinoptera bonasus*) (Orth 1975, Smith and Merriner 1985), spot (*Leiostomus xanthurus*) (Hildebrand and Schroeder 1928, Holland et al. 1980),

mummichogs (*Fundulus heteroclitus*) (Kelso 1979), whelk (*Busycon* spp.) (Peterson 1982, Irlandi and Peterson 1991), croaker (*Micropogonias undulatus*) (Hildebrand and Schroeder 1928), polychaete worms (*Nereis virens*) (Hidu and Newell 1989), and moon snails (*Polinices duplicatus*) (Edwards and Huebner 1977, Huebner and Edwards 1981). The feeding habits and seasonal changes in activity of these predators can alter the predation pressure on clams both inside and outside SAV and differ among clam life stages.

The ecological phenomenon of a biotic habitat in which animals utilize one area for resting and hiding and another area for feeding is not exclusive to SAV. Similar patterns have been seen in the activities of spiny sea urchins (*Diadema antillarum*) in patch reefs and grass beds in the West Indies. The sea urchins rest on the patch reefs in crevices during the day and nocturnally travel out away from the reef into the nearby turtle and manatee grass beds (*Thallasia testudinum* and *Syringodium filiforme*) to graze (Ogden et al. 1973).

Conclusions

In this study, the effects of a three-dimensional habitat (SAV), location with reference to that habitat, and seasons of the year have been explored as they affect the assemblage of clams that lives within the grass beds of the St. Mary's River. I found that in certain seasons SAV and location were both significant influences on the abundance of the clam

assemblage. Additionally, season was shown to be important in influencing the clam abundance found at these sites. These results provide another example of the complex and highly variable relationships between aquatic animals and their natural environments.

Chapter 3. Effect of submerged aquatic vegetation density on blue crab predation of soft-shell clams: Laboratory experiments using artificial seagrass

INTRODUCTION

Habitat complexity influences many ecological processes. Increased habitat complexity usually results in increased faunal abundances through a variety of mechanisms including increased access to food (Peterson et al. 1984), reduced exposure to environmental stress (Kohn and Leviten 1976), reduced predation risk (Orth *et al*. 1984, Wilson et al. 1987, Lubbers et al. 1990, Irlandi 1994), increased physical surface area in benthic habitats (Heck and Wetstone 1977), and decreased competition (Basquill and Grant 1998). Studies in coral reefs (Gorham and Alevizon 1989), coarse woody debris (Everett and Ruiz 1993) oyster beds (Lenihan *et al*. 2001), and submerged vegetation (Morgan 1980, Heck and Thoman 1981, Heck and Thoman 1982, Diehl 1988, Pohle *et al*. 1991, Irlandi 1994, James and Heck 1994, Skilleter 1994) have found that habitat complexity and the refuge value of habitat for prey organisms tend to increase simultaneously.

A number of studies have found that submerged aquatic vegetation (SAV) occurs in parallel with an increased abundance of a variety of invertebrate species (Heck and Thoman 1984, Orth and van Montfrans 1987, Rozas and Minello 1998, Castellanos and Rozas 2001) and finfish (Lubbers et al. 1990). For example, several species of decapod crustaceans were found in significantly higher densities in vegetated habitat compared to unvegetated habitat in Galveston Bay, TX (Scott-Denton 1999). Lobsters preferentially use eelgrass rather than bare mud as habitat in the Piscataqua River in New England, USA (Short *et al*. 2001). The Carolina marsh clam, *Polymesoda caroliniana* (Bosc), is more abundant where there are more plant stems than where the sediment is barren (Capehart and Hackney 1989). *Mercenaria mercenaria*, the hard clam, is found in higher densities within SAV than in sand flats adjacent to them (Peterson *et. al.* 1984, Peterson 1986).

Submerged vegetation provides protection from predators for aquatic invertebrates (Heck and Thoman 1982, Wilson *et al*. 1987, Wilson *et al*. 1990a, Wilson *et al*. 1990b). *Zostera marina* (eelgrass) canopy serves as protection for juvenile bay scallops, *Argopecten irradians* (Pohle *et al*. 1991). Survivorship of *M. mercenaria* is increased within vegetated habitats (Irlandi 1994). The suspension-feeding mussel, *Modiolus americanus*, benefits from increased survival within seagrass beds of *Thalassia testudinum* (Peterson and Heck 2001).

It has been suggested that predation on infaunal organisms is reduced in dense marsh and SAV habitats due to the increased difficulty of foraging between the plant blades (Heck and Orth 1980a, Kneib 1984, Graham *et al*. 1998). The root-rhizome structure in SAV is also critical in protecting infaunal estuarine animals by reducing the speed and efficiency with which predators dig into the sediment (Blundon and Kennedy 1982, Peterson 1982).

Some SAV beds, such as those formed by *Z. marina*, also increase food delivery to infaunal invertebrates (Peterson *et al*. 1984). Grass blades slow water currents causing more sediment and food particles to settle out of the water column in grass beds than in open sand flats (Ward *et al*. 1984). The increased food provision leads to increased growth rates that help *M. mercenaria* attain a shell size that reduces their susceptibility to predation at an earlier age (Peterson *et al.* 1984).

As clear as the beneficial relationship between aquatic invertebrates and vegetated habitat seems to be, there have been some published studies of systems where organisms in vegetation experienced increased mortality over conspecifics outside vegetation. Skilleter (1994) found that survivorship of both *Macoma balthica* and *Mya arenaria* were decreased within a *Ruppia maritima* bed. Beal (2000) found that survival rates of *M. arenaria* in eelgrass beds in Maine and of *M. mercenaria* in North Carolina grassbeds were reduced within the vegetation when compared to the adjacent sand flats. Another study revealed that the bay scallop (*A. irradians*) experienced higher predation pressure (>20% loss to predation/day) along the edge of the grass bed than within the bed or on

the adjacent sand flat (<5% loss to predation/day) (Bologna and Heck 1999). Another study found that even at high densities, artificial vegetation provided no refuge for *Mulinia lateralis* (little surf or coot clam) from predation by *Callinectes sapidus* (blue crab) (Orth and van Montfrans 1987).

I used controlled laboratory predator-prey experiments to test the hypothesis that crab predation on clams decreases with increasing SAV density. Predation rate may change due to the physical barrier that SAV roots and rhizomes create, and the physical as well as visual barrier that the blades form between crabs and clams.

METHODS AND MATERIALS

A series of experiments designed to test the effect of SAV on predator-prey interactions was conducted in mesocosm tanks using blue crabs (*C. sapidus*) as predators on juvenile soft-shell clams (*M. arenaria*) (Hines and Lipcius 1990, Hines *et al*. 1990). *M. arenaria* were chosen for these experiments because they were readily available from a local hatchery. *M. arenaria* is an infaunal bivalve abundant in intertidal and subtidal estuarine habitats from Maine to Virginia. It can bury itself up to 30 cm deep as an adult, although juveniles are found at much shallower sediment depths. It is a suspension feeder, extending its siphon just above the sediment surface. Blue crabs overlap in distribution

throughout the range of the soft-shell clam and feed on a wide variety of infaunal and epifaunal invertebrates as well as fish.

Four tanks (1.86 m long, 0.56 m wide, and 0.41 m deep) were set up in a laboratory of the Academy of Natural Science Estuarine Research Center (ANSERC), St. Leonard, Maryland. Water was supplied to tanks by a flow-through raw water system that utilizes water drawn from the Patuxent River Estuary, near the mouth of St. Leonard's Creek. Each tank had a sandy mud substrate approximately 20 cm deep that was made by mixing approximately equal volumes of mud collected from the mouth of St. Leonard's Creek and sand collected from Kings Reach Beach (Patuxent River Estuary) at Jefferson Patterson Park in St. Leonard.

Artificial SAV constructed to mimic *R. maritima* consisted of blades made from 5 mm wide green polypropylene ribbon (commonly known as curling ribbon) that was torn lengthwise into two or three pieces to make 1.7 to 2.5 mm wide blades (Fig. 15). This type of ribbon has been used to mimic SAV blades in many other studies (Keogh 1986, Almasi *et al*. 1987, Orth and van Montfrans 1987, Lethbridge *et al*. 1988, Sogard 1989, Sogard and Able 1994, Nemtzov 1997). The blades were approximately 15 to 20 cm in length and tied to a root and rhizome system made from artificial aquarium plants (Spanish Moss, Super Pet) that extended up to 8 cm into the sediment.

Two separate experiments were performed: a *single habitat* experiment and a *habitat choice* experiment. In the single habitat experiment, one density of SAV was planted within each tank. In the habitat choice experiment, there were three SAV densities planted in equal areas within each tank.

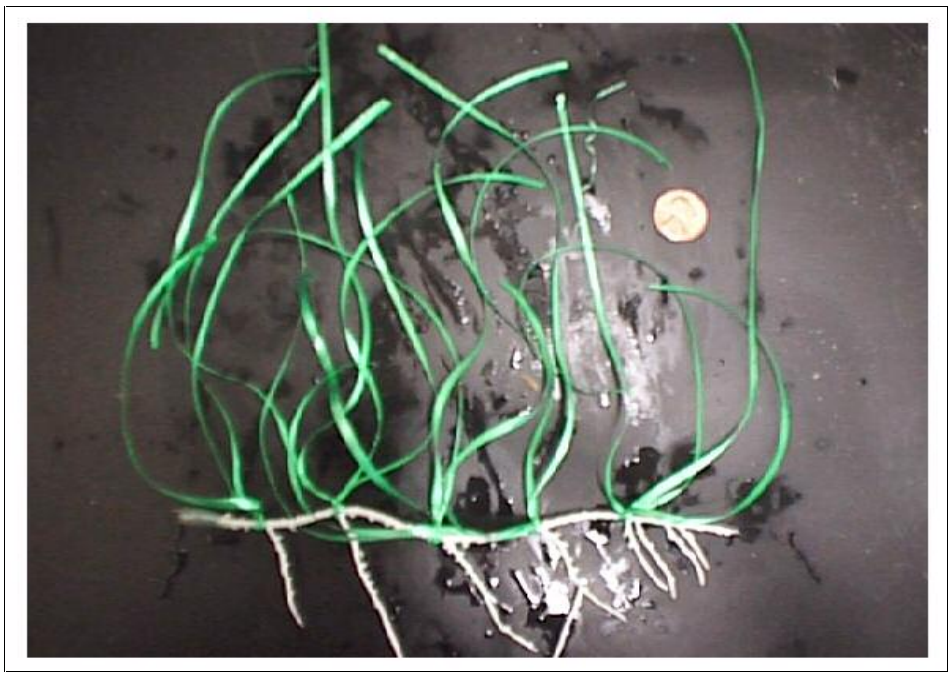

Figure 15. Photograph of artificial SAV representing five shoots.

Single Habitat Experiments

Null Hypothesis: The predation rate of crabs on clams will not change as SAV density increases when each crab is restricted to a single density habitat.

Alternative Hypothesis and Rationale: The predation rate of crabs on clams will decrease as SAV density increases. An increase in SAV density increases the barrier between crab and clams and should increase search time (locating and digging for clams).

Methods: Each tank was randomly assigned an SAV density and was planted with one density of SAV (0, 200, 1000, or 2000 shoots per m^2). These densities will be referred to as *no*, *low*, *medium*, and *high* SAV density treatments, respectively. Maximum field densities of R. maritima are similar to the high density treatment (Irlandi 1994, Irlandi 1997, Eggleston et al. 1998). Ninety measured juvenile *M. arenaria* with anteroposterior shell lengths of 14 to 40 mm were added to each tank, creating a density of about 90 clams per m^2, as used by Blundon and Kennedy (1982) and similar to field densities (Lipcius and Hines 1986). *M. arenaria* were obtained from Mid Penn Aquaculture (North, VA) on the Chesapeake Bay. After transport, clams were held in a tank with a sand substrate that was fed by the same water supply as used in the experimental tanks. The clams were placed approximately 3 cm deep in the sediment with their siphon ends pointed upward. They were given 16 hours to acclimate to this new habitat and to burrow before predators were added. Sixteen hours was chosen as the acclimation period in order to mimic that of a similar study (12 hours, Blundon and Kennedy 1982) and also allow for the same starting time for each run of the experiment.

At the end of the acclimation period, one terminal molt female blue crab (carapace width 124 to 165 mm) was added to each tank. Field densities of crabs have been reported to

be less than 1 per m^2 (Sharov et al. 2003). Terminal molt female crabs were utilized in an effort to remove fluctuations in feeding that occur during the molting process. Crabs were collected from the Chesapeake Bay area, held in tanks with a sand substrate and fed by the same water supply as the experimental tanks for no more than three days, and were starved for sixteen hours prior to introduction to the experimental tanks.

Tanks were provided with a 12 h: 12 h light cycle provided by banks of fluorescent light. Each experiment replicate ran for 48 h. At the end of 48 h, the crab was removed and released; crabs were not used in more than one replicate. Each tank was thoroughly searched for surviving clams and shell material from eaten clams. Surviving clams were enumerated and measured. Undamaged dead clams were assumed to have died during acclimation and were removed from the total number of clams recorded as offered to the crab in the experiment. Clams that were not found (dead or alive) were assumed to have been consumed by the crab. Five to six replicates of each SAV density treatment were completed for a total of 22 samples.

The statistical software utilized for all data analyses was SAS Version 8.0. All data analyzed using analysis of variance were examined and passed tests for normality, homogeneity of residual variances, and normality of residuals, except where noted. PROC MIXED was the procedure used for all ANOVAs, except where noted.

Linear correlation and one-way ANOVAs were conducted to determine if the lengths of clams or crabs used in the experiments were correlated or varied among SAV density treatments. In order to determine if there was a size preference by crabs, and if this preference varied among SAV treatments, I used an ANOVA to compare the difference in mean clam length of each group at the start and end of the experiment. An analysis of covariance (ANCOVA) was used to determine if crab size and/or SAV density treatments influenced the proportion of clams eaten.

Habitat Choice Experiments

Null Hypothesis: Clam consumption by crabs does not vary among SAV density treatments.

Alternative Hypotheses and Rationale:

1. The proportion of clams consumed by crabs will decrease with increasing SAV density. Crabs may preferentially feed in areas where detecting and digging up clams is easiest. The proportion of clams eaten should therefore be highest in the bare sediment treatment, lowest in the high density SAV treatment, and intermediate in the medium density treatment.

2. The predation rate (clams consumed per unit time spent in each habitat) of crabs on clams will decrease as SAV density increases. Handling time should decrease as

SAV density decreases and success (proportion of clams successfully excavated) should increase as SAV density decreases.

Methods: In the habitat choice experiments, crabs could allocate their time and feeding effort among three SAV densities. Sediment in each tank was physically separated into three equal areas using a plastic divider that extended from the bottom of the tank to 3 cm above the sediment surface. The purpose of the dividers was to separate the tank into three separate habitat areas and constrain the clams to the particular area in which they were placed, but to allow the crab to travel freely through all of the habitats.

Each tank area was planted with one of three treatment SAV densities (0, 1000, or 2000 shoots per m^2), so that each density was represented in each tank (Fig. 16). Three SAV treatments that matched the densities of the single habitat experiment (no, medium, and high) were used instead of all four SAV treatments due to the limited area of the tank bottom. The position of each of the three densities of SAV was assigned randomly within each tank.

Thirty juvenile *M. arenaria* (17.3 – 40.2 mm in length) from the same source and holding conditions as the single habitat experiments were placed in each tank area, creating a density in each habitat of about 90 clams per m^2 as done by Blundon and Kennedy (1982). Clams were provided with a 16-hour period, as in the single habitat experiments, in which to acclimate, bury themselves, and begin to feed.

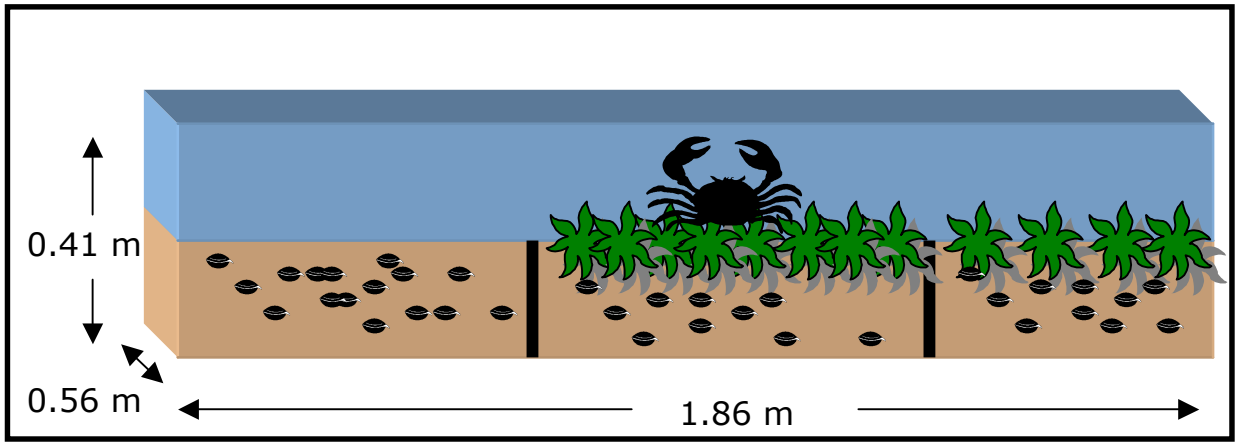

Figure 16. Schematic of a tank setup for the choice habitat experiments, showing one crab, a random placement of three SAV densities into separated areas within the tank, and clams buried into the sediment in each of the three areas.

One terminal molt female blue crab (carapace width of 135 to 151 mm) that was held and starved as in the single habitat experiment was placed in each tank. The predation period ran 48 hours at which point the crab was removed and released. Each tank was thoroughly searched for surviving clams and shell material from eaten clams. Surviving clams were enumerated and measured. Undamaged dead clams were assumed to have died during acclimation and were removed from the total number of clams recorded as offered to the crab in the experiment.

The amount of time that each crab spent in each of the three habitats was determined using video cameras. A predation rate was calculated using the number of clams

consumed in each habitat (normalized to thirty clams offered) divided by the total experiment time spent in that habitat. Because there were times when the crab could not be located due to turbid water or taping problems, the total experiment time spent in each habitat was calculated from the proportion of time spent in each habitat over the total time the crab was tracked on tape multiplied by the total experiment time (48 h).

To videotape crabs under low light and turbid conditions, each crab was fastened with a harness made of three small (2.5 cm) glow-light sticks held together using rubber bands and attached to the spines of the carapace with rubber bands in a backpack like fashion (Fig. 17). As the burn time of the glow sticks is approximately 5 hours, the backpacks were changed several times during the experiment. Each crab was removed, had her backpack replaced with a new one, and placed back in the tank in the location at which she was found. This process took no more than two minutes and each crab was treated with the same number of backpack changes.

In order to examine if the low light emitted by the glow sticks altered the feeding behavior of the crabs, two replicates of the experiment were run with crabs that were wearing glow stick backpacks that had already burned out. These replicates were treated with the same number of backpack changes, but each time the crab received a backpack with glow sticks that were not illuminated. Because I was unable to videotape crabs without light-emitting glow sticks, the data collected from these replicates was used only

to determine whether the crabs ate similar numbers of clams as crabs wearing illuminated backpacks.

Figure 17. Photograph of the backpack light source used in the habitat choice experiments to record the crab's location throughout the experiment.

In the habitat choice experiments, the resulting proportions of clams eaten from each of the three habitats by one crab in one tank were not independent of one another. The proper analysis for multiple measurements from one unit where independence cannot be assumed is the multivariate analysis of variance or MANOVA (Sokal and Rohlf 1995). Therefore, a MANOVA was used to determine if the proportion of clams consumed varied among SAV treatments. The model for this analysis was:

$$MEDvNO\ HIGHvNO = 0$$

where MEDvNO = the difference between the proportion of clams eaten in the medium density SAV habitat and the no SAV habitat

HIGHvNO = the difference between the proportion of clams eaten in the high density SAV habitat and the no SAV habitat

These two values were simultaneously compared to zero. If neither of them were significantly different from zero, then no significant differences existed among treatments.

Because the proportion of time spent in each habitat would total to one (1) for each crab (i.e., $P_{high} + P_{med} + P_{no} = 1$), a logratio analysis of composition model was utilized to test whether the crabs spent significantly different proportions of time in each SAV density (Aitchison 1986):

$$HIGHvMED = \log (P_{high}/P_{med})$$

$$MEDvNO = \log (P_{med}/P_{no})$$

$$HIGHvMED\ MEDvNO = 0$$

where HIGHvMED = the difference between the proportion of clams eaten in the high-density SAV habitat and the medium-density SAV habitat

MEDvNO = the log of the ratio between the proportion of clams eaten in the medium-density SAV habitat and the no SAV habitat

As in the test of the proportion of clams eaten, these two values were simultaneously compared to zero. If either of these two values were found to be significantly different than zero, an additional MANOVA was run on MEDvNO and HIGHvNO. A log ratio MANOVA was also used to analyze the differences among SAV treatments in the ratio of clams eaten per unit time.

Additional tests were used to check for potential sources of bias in experiments and to examine the potential for size-based preferences in crab predation. Regression analyses were used to examine the relationship between crab length and the total proportion of clams consumed in the tank ($P_{high} + P_{med} + P_{no}$), and the relationship between crab length and proportion of time a crab spent in the habitat without SAV. In order to determine if there was a size preference by crabs, and if this preference varied among SAV treatments, I used an ANOVA to compare the difference in mean clam length of each group at the beginning and end of the experiment. One-way ANOVA was used to test whether mean size of consumed clams varied among SAV treatments.

RESULTS

Single Habitat Experiments

Clam length frequencies for each SAV habitat type are shown in Figure 18. Because clam length distributions were bimodal, tests of clam length were done on rank-transformed data. A nested ANOVA on rank-transformed clam length data (SAS PROC MIXED model: Length of individual clams= Tank + SAV treatment (Tank)) indicated that there was no significant difference in clam lengths among SAV treatment groups ($F = 0.53$, $p = 0.67$; Fig. 19). Clam length averaged 28.2 mm $\pm$ 0.14 mm across all treatments, with only 1.25 mm separating the largest and smallest mean clam size. A linear correlation indicated that clam length and crab length were not correlated (Pearson Correlation Coefficient = 0.016, $p = 0.95$).

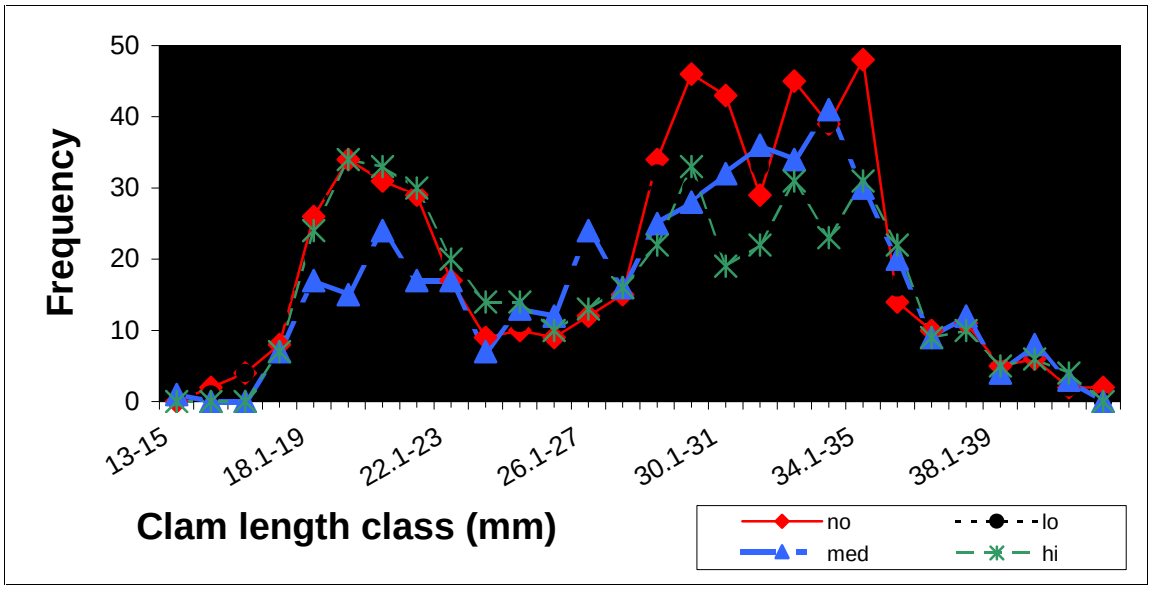

Figure 18. Clam length frequencies by SAV habitat treatment.

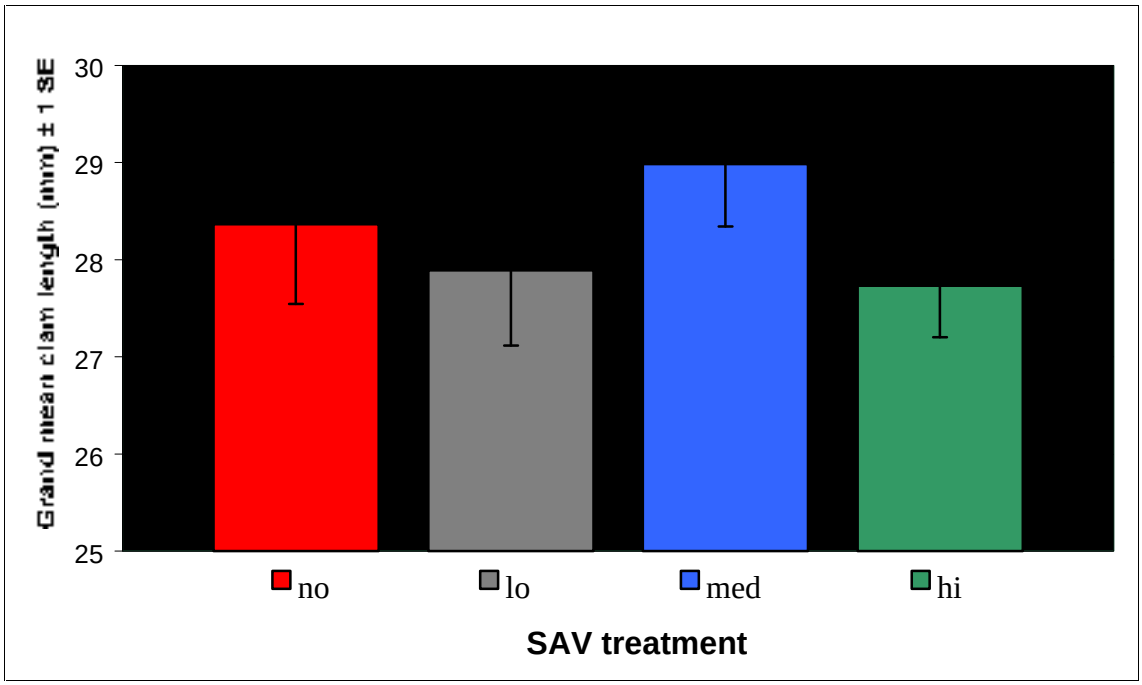

Figure 19. Grand mean clam length (calculated from tank means) by SAV habitat treatment.

The change in mean clam length was less than 1 mm for all treatments and did not differ significantly among SAV density treatments ($F = 0.73$, $p = 0.55$). A simple linear regression also indicated that there was no significant relationship between change in mean clam length and crab length ($r^2 = 0.07$, $p = 0.29$).

Analysis of covariance (ANCOVA) was used to determine whether the proportion of clams eaten from each tank was affected by SAV density treatment or crab length. The interaction between SAV density treatment and crab length was not significant ($p = 0.96$). The initial analysis of covariance (ANCOVA) considering all four separate SAV

treatments indicated that crab length significantly affected the proportion of clams eaten ($F = 10.77$, $p=0.004$; Fig. 20). Clam consumption did not differ among SAV treatment ($F=1.99$, $p=0.153$; Fig. 21). Because mean clam consumption in all three with-SAV treatments was lower than that in the no-SAV treatment, however, I also used a contrast statement to test for a difference between tanks with and without SAV. Results indicated that consumption was significantly higher in the absence of artificial SAV ($F=5.12$, $p=0.037$). I therefore reran the ANCOVA including the fixed effect of SAV presence (i.e., presence vs. absence of SAV) with crab length as a covariate. This final test indicated that the proportion of clams eaten was significantly greater in the absence of SAV than with SAV present ($F = 5.39$, $p = 0.032$). As in the initial test, the proportion of clams eaten significantly decreased with increasing crab size ($F = 12.82$, $p = 0.002$).

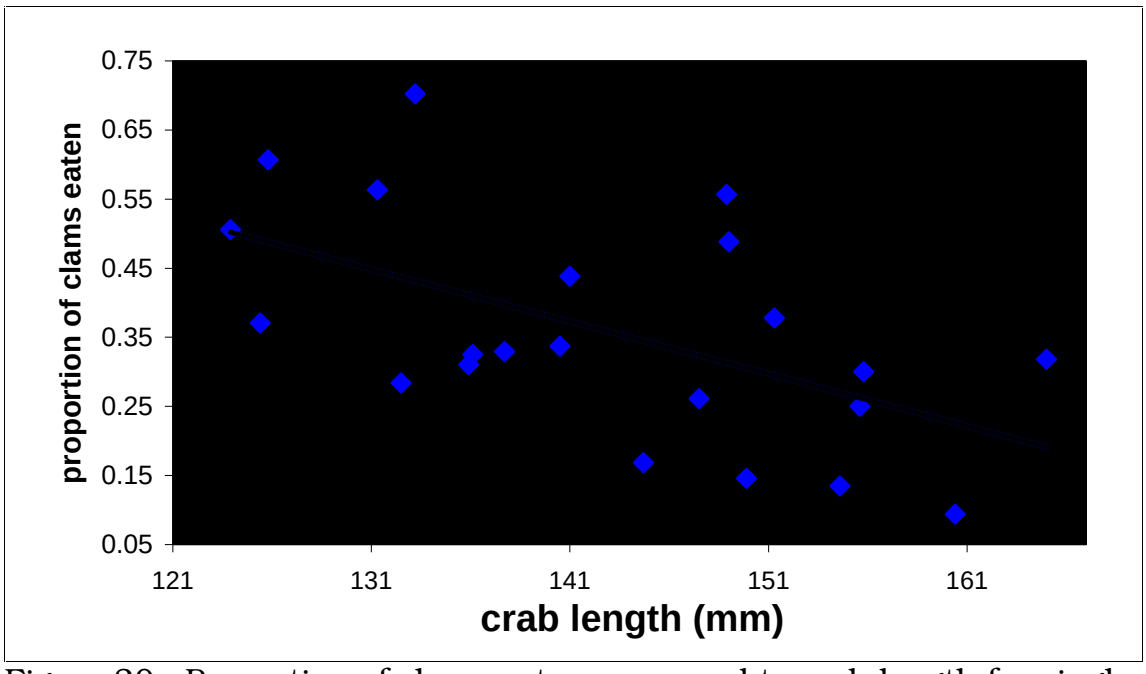

Figure 20. Proportion of clams eaten compared to crab length for single habitat experiments.

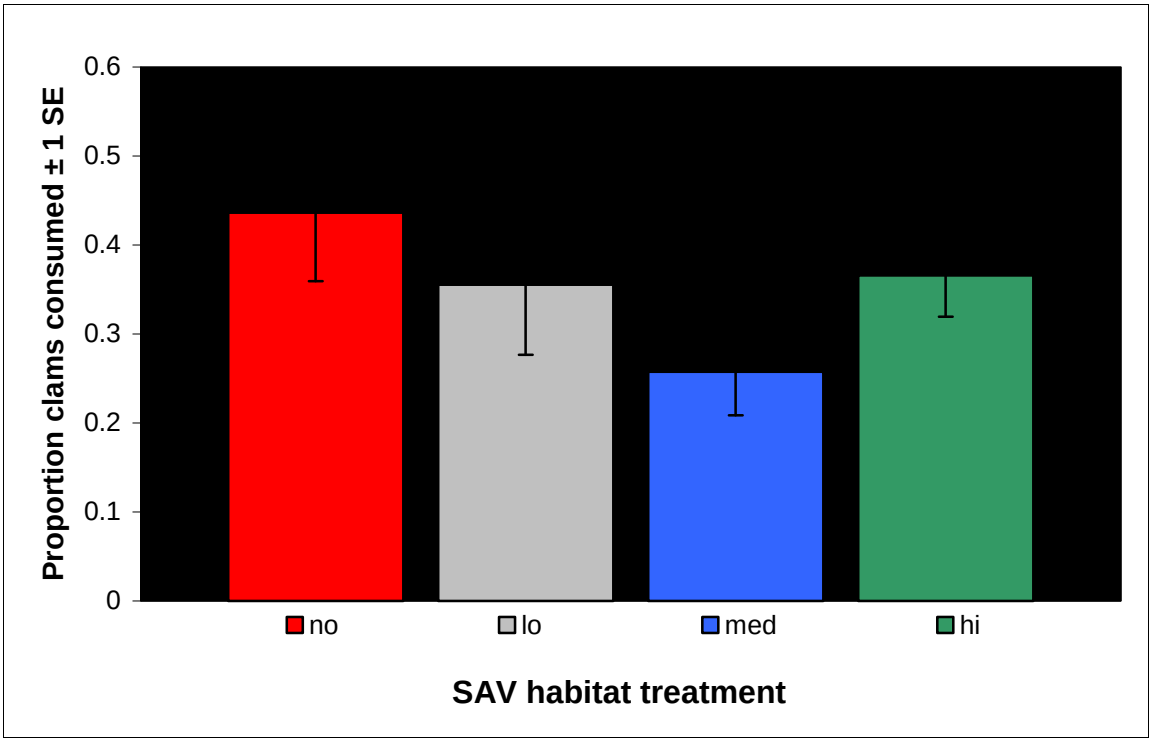

Figure 21. Mean proportions of clams eaten from each SAV habitat treatment.

Habitat Choice Experiments

A nested design ANOVA (SAS PROC MIXED model: Length of individual clams= SAV treatment + Tank (SAV treatment)) on rank-transformed clam length data showed that there was no significant difference in clam lengths among SAV treatments ($F = 0.29$, $p = 0.75$; Fig. 22). Clams used in this experiment averaged 29.16 mm ± 0.25 mm in length. In an ANOVA, the difference in tank mean clam length was not significantly different from zero (0.12±0.24 mm; $F = 1.08$, $p = 0.36$).

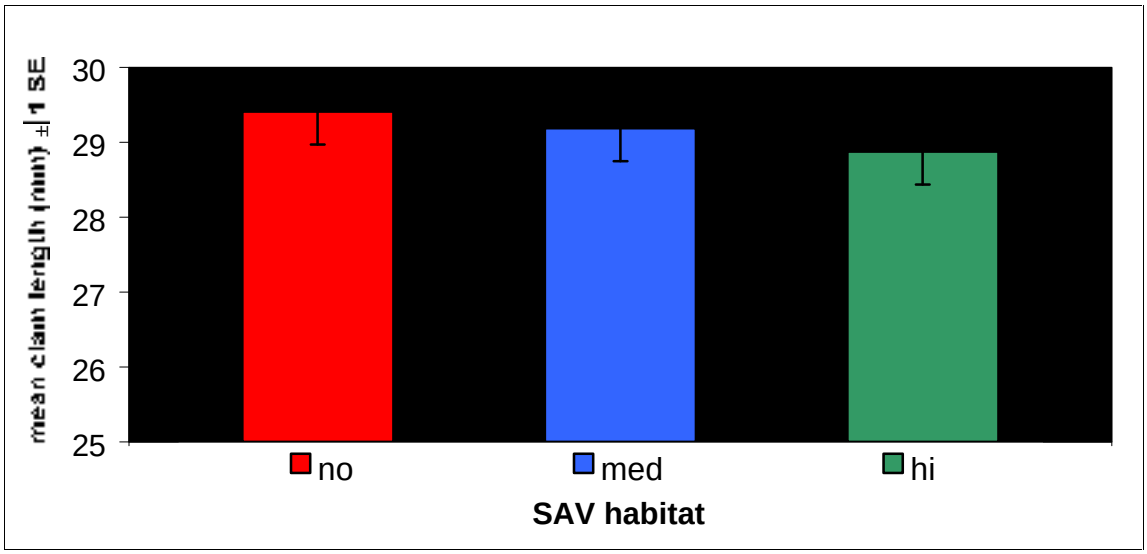

Figure 22. Grand mean clam length by SAV treatment for habitat choice experiments.

An initial MANOVA considering no, medium, and high SAV as three separate treatments indicated that there was no significant difference among the three SAV density treatments in the proportion of clams eaten (high versus medium: $F = 0.60$, $p = 0.47$; medium versus no: $F = 4.27$, $p = 0.09$; high versus no: $F = 6.26$, $p = 0.054$; Fig. 23). However, there was a strong trend toward lower clam consumption in both vegetated SAV treatments than in the absence of SAV (medium versus no: $p = 0.09$ and high versus no: $p = 0.054$). I therefore performed a second test that combined the two vegetated SAV treatments. This second analysis indicated that a significantly lower proportion of clams was consumed in vegetated habitats than in the unvegetated habitat (0.23 ± 0.06 vs. 0.47 ± 0.08; $F = 6.30$, $p = 0.023$).

Regression indicated that the relationship between the proportion of clams eaten from a tank (i.e. three SAV habitats) and the crab length was both weak ($r^2 = 0.1509$) and not significant ($F = 0.71$, $p = 0.45$; Fig. 24).

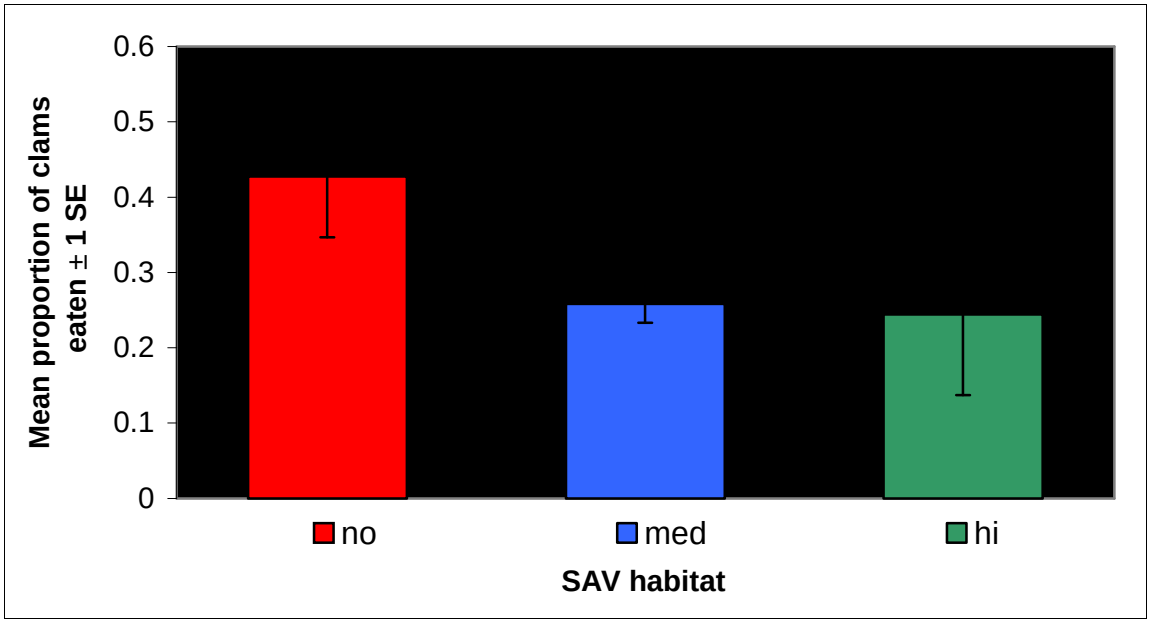

Figure 23. Mean proportion of clams eaten from each SAV habitat type in habitat choice experiments.

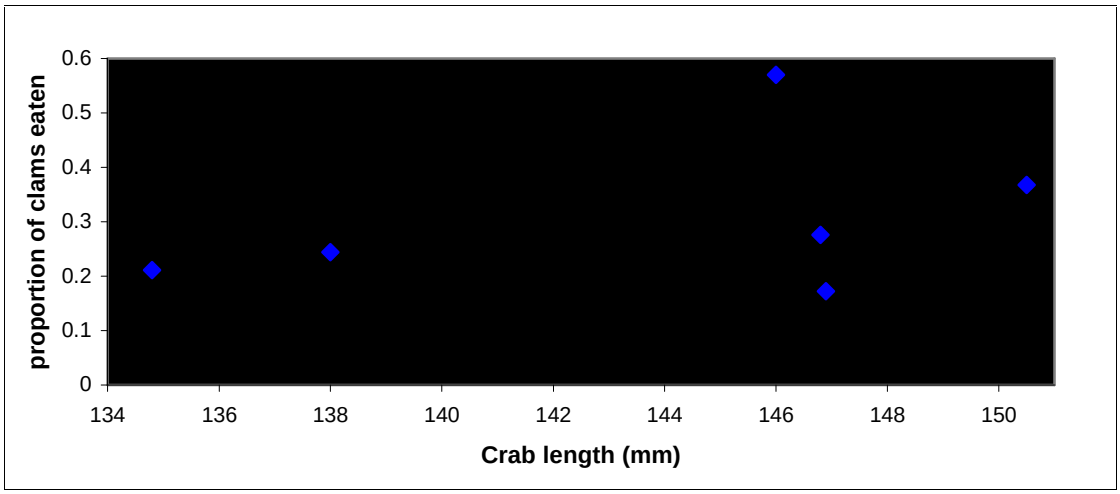

Figure 24. Regression of proportion of clams eaten from tank by crab

length.
The mean proportion of time that the crabs spent in each habitat is shown in Figure 25. A MANOVA indicated that crabs spent a significantly greater proportion of time in the medium SAV density habitat than the no SAV habitat ($F = 15.07$, $p = 0.012$). The other two comparisons (high SAV density habitat to medium SAV density habitat and high SAV density habitat to the no SAV habitat) were not significantly different ($F = 2.95$, $p = 0.15$ and $F = 2.08$, $p = 0.21$).

Because large crabs might be less reliant on SAV as refuge from predators, the relationship between the time that crabs spent in the open area (or no SAV habitat) and crab length was examined. The regression analysis showed that this relationship was both weak ($r^2 = 0.024$) and not significant ($F = 0.10$, $p = 0.77$; Fig. 26).

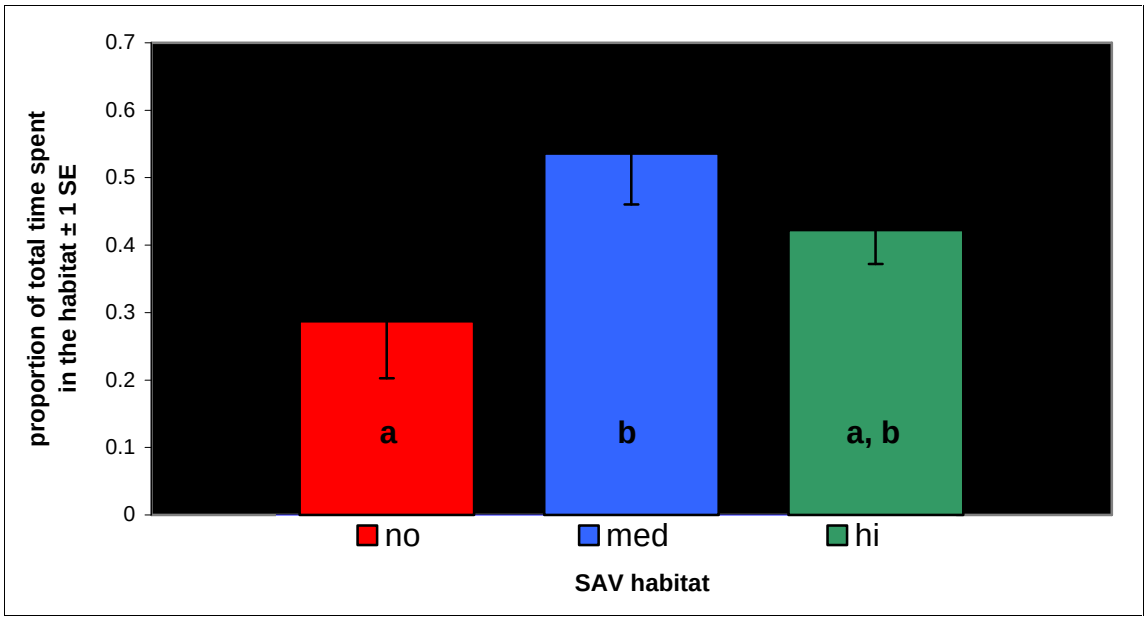

Figure 25. Mean proportion of time that crabs spent in each of the three SAV density habitats in the habitat choice experiments. Different letters represent significant differences among SAV density habitat treatments.

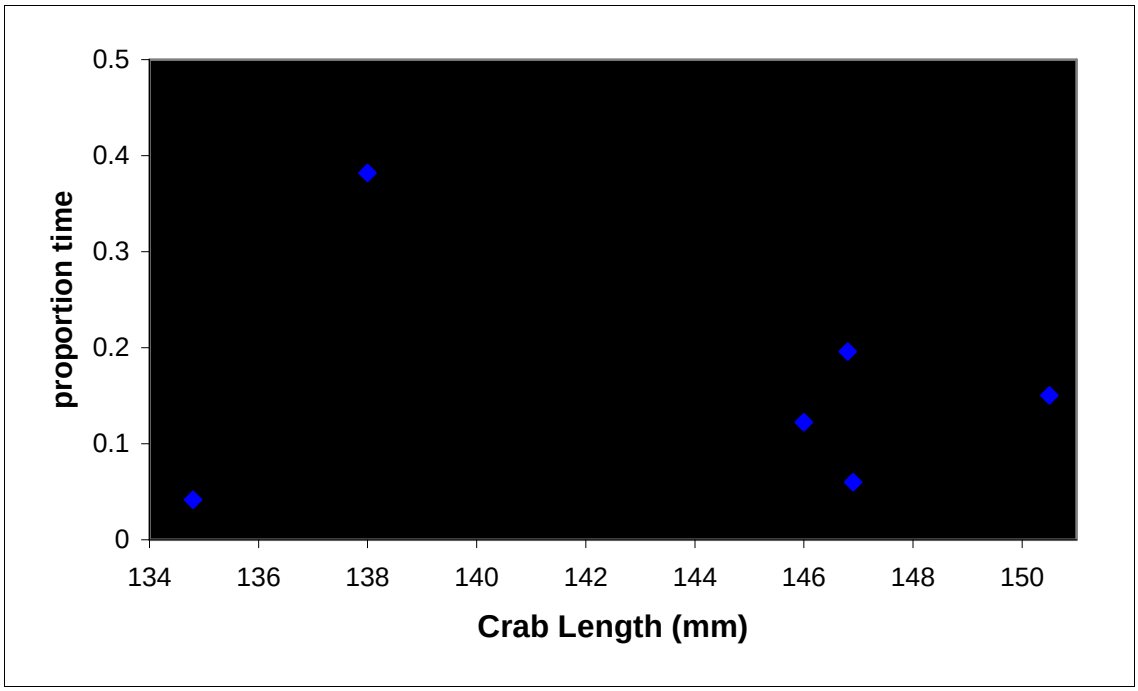

Figure 26. Regression of the proportion of time that the crab spent in the no SAV habitat versus crab length.

The null hypothesis that the predation rate of crabs, defined as the number of clams eaten divided by the number of hours spent in that habitat, does not change among SAV density treatments was tested with a MANOVA that utilized a logratio analysis of composition. The model was similar to that used for time allocation analysis, except that the proportion of time was replaced by the predation rate in each of the three habitats. The predation rate in the medium SAV density treatment was significantly lower than the predation rate in the no SAV treatment ($F = 10.21$, $p = 0.03$; Fig. 27). Mean predation rate in high SAV density treatment was less than one-fourth that in the absence of SAV, but the difference was not significant ($F = 5.30$, $p = 0.08$). Predation rates in the two vegetated treatments were similar ($F = 1.28$, $p = 0.32$).

A second analysis combining the two vegetated SAV treatments indicated that there was a significant difference between vegetated habitats and the unvegetated habitat in the predation rate of crabs on clams ($F = 16.14$, $p = 0.001$). Crabs ate an average of 2.86 ± 0.88 clams per hour spent in the unvegetated habitat compared with only 0.47 ± 0.14 clams per hour in either vegetated habitat.

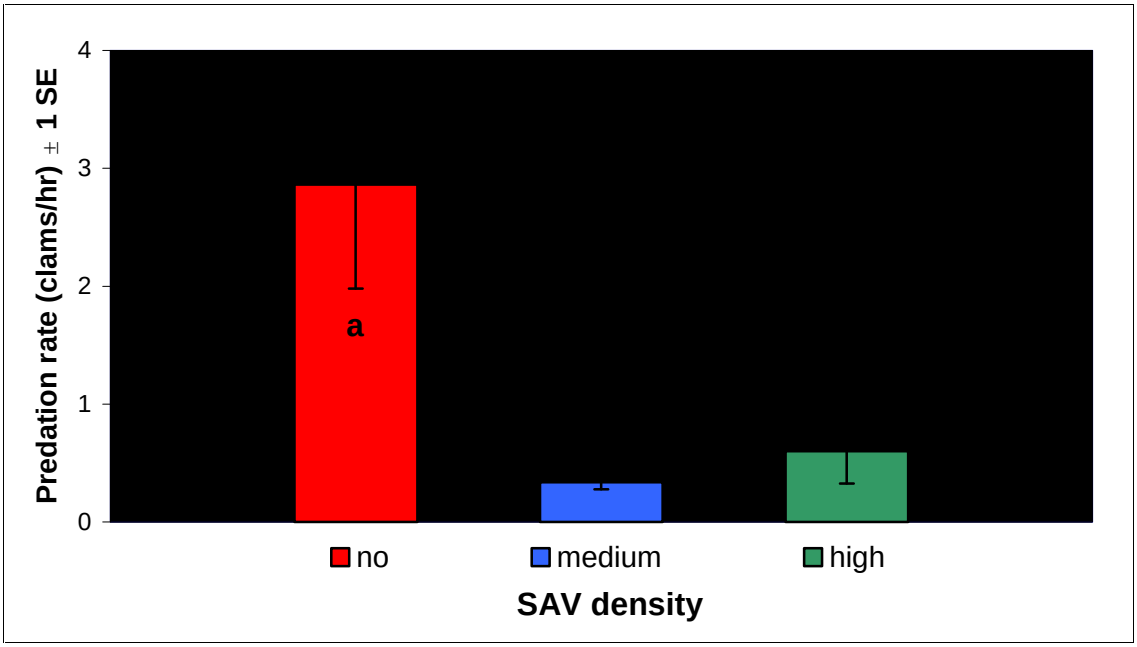

Figure 27. Crab predation rate on clams (in clams/ hour) by SAV density treatments. Different letters represent significant differences among SAV density habitat treatments.

DISCUSSION

Laboratory experiments using artificial SAV indicated that SAV presence has the potential to strongly influence habitat use and predation rates of blue crab feeding on soft-shell clams, and predation mortality of the clams. Results indicated that predation rates and mortality were increased in unvegetated habitat, both in single habitat experiments and when predators were offered the opportunity to choose among different habitat types.

Single Habitat Experiments

The single habitat experiments were performed to examine the differences, if any, among crab predation on clams in a habitat containing a single density of SAV. The null hypothesis, that crab predation would not vary with differences in habitat, was rejected. The density of the SAV did not affect clam consumption, but the presence of SAV did significantly decrease the proportion of clams consumed in the single habitat experiments. This showed that some aspect of SAV habitat was decreasing the crab consumption on clams, even though these crabs did not have an alternate habitat in which to feed.

One interesting finding in the single habitat experiments was that crab length influenced the proportion of clams eaten. This result was counterintuitive in that the proportion of clams consumed decreased as the crab carapace width increased. There is no straightforward explanation for this result. Terminal-molt female crabs were used because molting has an effect on the feeding activities of crabs (Freire and Gonzalez-Gurriaran 1995, Mantelatto and Christofoletti 2001). However, ovigenerous crabs of the family Portunidae have been shown to alter their eating habits during certain stages of reproduction (Freire 1996, Mantelatto and Christofoletti 2001). Although crab reproductive stage was not determined for the crabs used in this experiment, this fact may have driven some of the differences seen in consumption.

Habitat Choice Experiments

In the experiments that offered crabs a choice of three SAV densities, a lower proportion of clams were consumed in the vegetated habitat compared to the unvegetated habitat. The proportion of clams consumed by crabs was 1.7 times higher in unvegetated habitat than in the presence of artificial SAV. However, the specific density of SAV did not affect crab predation. Crabs may have had a harder time locating prey among the grass blades in the vegetated habitats as has been seen in other studies with crabs (Heck and Orth 1980a, Kneib 1984) and finfish (Savino and Stein 1982, Graham *et al*. 1998).

There was also a significant difference between the amount of time that the crabs spent in the no SAV habitat and the medium-density SAV habitat. Overall, the crabs spent 84 percent of their time in the vegetated habitats. The time spent in the two vegetated habitats did not differ significantly. In the field, SAV may protect crabs from predators. The crabs in my lab experiment may have been spending the majority of their time in the vegetated habitats in order to avoid being detected by predators. Identifying this behavior as avoidance of visual predators is uncertain, however, because the data indicated that crabs spent equivalent proportions of time in the no SAV habitat during the day versus night (day = 0.13 ± 0.04 and night = 0.18 ± 0.06).

Predation rates were highest in the habitats in which the crabs spent the least time. The predation rate in the no SAV habitat was nearly an order of magnitude higher than the rate in the medium-density SAV habitat. A further analysis comparing unvegetated

versus vegetated habitats shows that predation rate was significantly lower in the vegetated habitats than in the absence of SAV. Crabs in this experiment generally spent the majority of their time inactive in the vegetated habitats and moved into the unvegetated habitat to feed and quickly return to the vegetation. These results complement those of field studies that also found blue crab abundances significantly higher in SAV habitat than in unvegetated habitats (Heck and Orth 1980b) and predation rates on crabs that were higher in bare sand bottom than in eelgrass beds (Wilson et al. 1987).

Artificial SAV

The use of artificial seagrass in these experiments may have had an effect on the feeding behaviors of the crabs and burrowing of the clams. Several studies have utilized artificial SAV to mimic natural seagrass (Barber et al. 1979, Bell *et al*. 1985, 1987, 1988, Shulman 1985, Sogard 1989, Sogard and Able 1994, Boström 1999, Priyadarshana 2001). Artificial SAV is utilized and inhabited similarly to real SAV by planktonic invertebrate settlers (Bell *et al*., 1985, 1987, 1988) and settled aquatic invertebrates and finfish (Sogard 1989). One potentially significant difference between artificial and natural SAV is the abundance and species composition of the epiphytic algae that colonizes the grass blades (Sogard 1989). Even though crab may have not utilized artificial SAV in these experiments exactly the same way that natural SAV would have been used, the video surveillance and data showed that all habitat types were explored in

the experiments and I believe the overall results are qualitatively similar to what would be seen in the field.

Conclusions

In summary, crab consumption of clams decreased in the presence of artificial SAV, whether or not the animals had an alternate habitat in which to feed and in spite of the fact that crabs were successful at finding and obtaining food whether SAV was present or absent. The effect of artificial vegetation on clam consumption was strongest in the habitat choice experiments.

These experiments support the hypothesis that crabs prefer to feed from areas free of vegetation, while spending that majority of their time in vegetated areas. This behavior allows them to feed in less energetically "expensive" conditions, where locating and excavating prey are minimized, and to maximize the benefits of predator avoidance provided by the complex habitat. For clams, the refuge created by SAV is significant in their survivorship from crabs.

The relationships between aquatic animals and their natural environments can be complex and highly variable, and influenced by numerous factors. These results should contribute to a better understanding of a portion of the intricate relationships among decapods, infaunal bivalves, and their vegetated habitats.

Chapter 4. Conclusions

The results of my research suggest that SAV habitat influences survival of infaunal clams. In the field, I found at my study sites in spring, SAV biomass and location with respect to the grass bed did not significantly influence clam abundance or distribution. This can potentially be explained by the fact that predation activity had not yet increased to its full potential by the time the spring sampling events occurred. However, predation is still present during spring and the trend toward higher abundance inside the grass bed mimicked that seen in the summer samples. The high variability in clam abundance and weaker trend may have required a larger sample size to see a significant effect. In the summer and seasonal analyses, SAV biomass significantly influenced clam abundance. By summer, predator activity has increased over that in the spring and predation pressure on infaunal clams is extremely heavy. I suggest that SAV is providing infaunal clams protection from heavy predation pressure during summer and this is the reason that abundance was significantly higher in higher SAV biomass.

Since I did not directly test predation differences between spring and summer, there is also a possibility that predation pressure had not increased between the two seasons and

the differences in the magnitude and variability of clam abundance in high and low SAV locations are instead being driven by the fact that more time has passed since recruitment by the time summer sampling events occurred than by the spring sampling events. Predators would have had more time to prey on the same populations of clams in the grass beds so that the spatial pattern caused by the effects of predation were more clearly defined in the summer samples. It should be noted that differences between the abundances seen in the spring and the fall cannot be attributed to new settlement because these clam species spawn in the early spring (before my spring sampling dates) and in the late fall (well after my summer sampling dates).

The suggestion that predation pressure is greater outside the grass bed is supported by the crab pot data that I collected and analyzed. The crab pot data revealed that crab abundance (when drawn toward food) was significantly greater outside SAV compared to abundance inside SAV. Although studies have shown the opposite trend in crab abundance, I propose that crabs rest and hide in SAV during the day to obtain the same protection that clams are deriving from this habitat, and travel into adjacent sand flats when they want to feed because it is easier to dig in sand as opposed to SAV for food. While traveling in sand flats and searching for food, they were attracted to the crab pots by the bait and were caught.

These conclusions are further supported by the results of my laboratory experiments, which showed a greater consumption of clams in unvegetated habitat compared to that of

the habitats with SAV. This difference was seen in both single habitat and habitat choice experiments. And finally, this hypothesis is also supported by the fact that in the habitat choice experiments, the crabs spent a disproportionate amount of time in the vegetated habitats compared to the proportion of food they consumed from those habitats.

In summary, this research supports the published work of those who found that SAV habitat is important to the survivorship of infaunal clams under predation pressure (Blundon and Kennedy 1982; Crockett 1989; Irlandi and Peterson 1991; Irlandi 1994, 1997) and counters those studies which report that clam mortality is increased inside SAV (Orth and van Montfrans 1987, Skilleter 1994, Beal 2000). In St. Mary's River, clam abundance in SAV is seasonally variable and is reduced in summer with decreasing SAV biomass. This pattern is probably due to seasonal differences in predation pressure.

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